

EAST AFRICAN MAMMALS

An Atlas of Evolution in Africa

Volume IIIC

Jonathan Kingdon



Academic Press



For fifteen years Jonathan Kingdon studied and portrayed the wildlife of Kenya, Uganda and Tanzania. Since 1971 his work has been published in a series that has gained international acclaim as one of the most remarkable zoogeographical studies of our time — *East African Mammals*. In successive volumes the primates, small mammals, and latterly, large mammals, have been subjected to the exhaustive scrutiny of a dedicated observer. Details of behaviour and anatomy undetected by the camera have been captured in exquisite and vital line drawings and sketches. A wealth of information on physiology, distribution, social systems, habitat, ecology and evolution has been encapsulated in a penetrating and commanding text. Taken individually, the volumes of *East African Mammals* provide the most comprehensive guides available for their particular subjects: taken together they make up a treatise of immeasurable value, which culminates in this two-part volume on the bovids.

In considering over 40 species of East African bovids, Jonathan Kingdon offers not only new information but also a new approach to this group of mammals. Thus original information on, for example, dwarf and hippotragine antelopes, forest duikers, bongo and hartebeest is set in the context of a fresh approach to the bovid family as a whole, which is presented for the first time as a single evolutionary radiation. In addition, the confusing area of bovid taxonomy is re-appraised, and a simple classification of subfamilies and tribes based on recent ecological and palaeontological research is proposed. As in previous volumes, there is considerable emphasis on the relationship between form and function; body architecture and size, horn shape, coat pattern and tooth structure are some of the aspects that are discussed in a broad comparative, ecological and evolutionary context. Further understanding of bovid ecology and evolution should have far-reaching effects on animal husbandry and range management in Africa, at present largely based on practices developed in more temperate climates.

Throughout the text Jonathan Kingdon displays a rare ability to combine a thorough and critical exposition with an intuitive understanding of his subject, perhaps best displayed in his beautiful and sensitive drawings. In all the volumes of *East African Mammals* his concern for the fauna of this tropical region is paramount. As the ancient links between Man and animal are broken down, and Man becomes careless of his environment and the multiplicity of species it fosters, the mammals of East Africa, and indeed the entire continent, are threatened. Understanding can only be restored through knowledge of the evolution, biology and ecology — and hence needs — of these species: few books are more likely to pave the way than *East African Mammals*.

"I have nothing but praise for this book . . . It is indispensable, both for our knowledge of the East African mammalian fauna, its habits and its geological history, and also for indicating what gaps in our knowledge, especially of their behaviour, remain to be filled. I commend it to all serious students of African ecology, both for the beauty of its illustrations and for its biological thoroughness."

Sir Julian Huxley
from a review of Volume I

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EAST
AFRICAN MAMMALS

Jonathan Kingdon

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An Atlas of Evolution in Africa

Volume III Part C (Bovids)



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I hope that some of the members of the Wildlife Clubs' Movement, especially in Kenya and Wildlife Departments in all three countries will have the opportunity to see these volumes, their enthusiastic participation in recording the distribution of some important mammal species has been greatly appreciated, is a valuable contribution and a hopeful augur for the future.

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Bovids, Horned Ungulates

Bovidae

Sub-families

Bovinae

Antilopinae

Contemporary agriculture is developing techniques that are turning over an ever larger proportion of the world's primary production to our own use. Apart from the relatively small number of fruit, vegetable and cereal species that we grow and consume directly, we use a vast number of grass and other plant species indirectly by way of three bovid species which convert them into products we can use.

There are several reasons why the 50 odd species of wild bovids described in this volume need to be seen in the context of our dependence on cattle, sheep and goats.

First the importance of these three species lies in the efficiency with which they convert vegetation into meat, milk, hide and harnessed energy. In many natural circumstances other species are demonstrably superior to livestock in the very faculties for which we value them and there are profound ecological reasons why this should be so. Continual study of all surviving bovid species and their habitats is necessary, not because we are likely to embark on further large-scale domestication, but because we are deeply ignorant of the processes which we have shrewdly but blindly exploited all these long centuries. Our livestock, now isolated in their pens and paddocks were taken out of an ecological matrix of which we know very little, and the chances of putting them in some sort of evolutionary and historical perspective (which should be a scientific imperative), diminishes progressively with the decline and extermination of their nearest relatives and the degradation and impoverishment of their natural habitats.

All over the world men in their millions invest land, money and lives in still more millions of cattle and sheep; there are countless veterinary and husbandry institutes; millionaires bulldoze the forests of Amazonia to ranch cattle; international agencies finance merino sheep on African equatorial mountains; economists and farmers sing their praises; herdsman and poets sing their praises; our language is redolent with the symbolism of bulls, lambs and the pastoral life. Cults of the cow or sheep dominate the existence of entire communities and nations, not only in Masailand and the Sudd but in Argentina, New Zealand, Central Asia and Texas, to name but a few.

Yet the immense vested interests that feed on this exploitation of bovids have shown no interest in, nor supported any one of the small band of scientists that have contributed most to our present knowledge of bovid ecology, the comparative anatomy of rumination, comparative behaviour and the study of bovid origins.

Opposite: Lesser kudu, *Tragelaphus imberbis*.

This is not only a failure of self-interest or a lack of curiosity: it is a larger failing in the quality of our imagination. If we have been unable to peruse the physical form or ponder on the day to day existence and history of these familiar animals can we be adequately equipped to explore our own existence and past in this same world of time and space?

Of course the bare facts are reasonably well known and documented. Cattle, sheep and goats evolved in Eurasia, which is where they were originally domesticated. Some of their wild relatives still continue a precarious existence in the mountains or remaining forests of Asia, and Schaller (1967, 1977) has written moving accounts of those dying worlds.

In the fossil beds and archaeological excavations of India, China, the Middle East and southern Europe there lies a fragmentary, disjointed but immensely long history revealing that from an Asiatic tragulid stock deer, giraffes, pronghorns and finally, in the Oligocene, bovids emerged. In the Asiatic steppes and jungles these various ruminants competed with equids, rhinoceroses, tapirs and smaller herbivores, and the texture of Eurasian faunas from the Miocene to the present implies that competition from these antecedent herbivores has always put limits upon bovid evolution. It was from these peculiar communities that our domestic species were plucked.

In Africa the story has been very different. Here the primitive bovids probably entered at about the end of the Oligocene; with only archaic herbivores such as the anthracotheres, hyracoids and proboscids to compete with, they were therefore free to move into a much wider range of herbivorous niches.

In the 20 million years since that invasion, relationships have evolved between the vegetation and this one family of herbivorous mammals that cannot be matched anywhere else on earth for their complexity or efficiency. To analyse just how so much energy is trapped and cycled between so many interacting organisms; to reconstruct and model those orderly processes whereby these communities have developed and continue to regulate themselves; to understand how such communities interact to produce those dynamic patterns of change that we call ecological successions; these are urgent priorities for Science in Africa.

In large part they are urgent priorities because the international livestock industry, unable to focus beyond a pen, fence or ranch boundary, not only fails to support fundamental research on bovids and their ecology but, in one way or another, promotes massive interventions in tropical Africa. Plains have been fenced, water tables lowered, pastures stripped, trees felled and insecticides sprayed over very large areas (see p. 592). Millions of wild bovids have been systematically destroyed without a thought even for the scientific value of the slaughtered populations (p. 592). Unless the industry's ecologically blinkered attitudes can be reformed, its unfettered progress must ultimately threaten the existence of most of the unique wild herbivore communities. That the sorcerer's apprentice is releasing forces he is unable to comprehend is already evident in the Sahelian region.

Much ecological research is taking place in many parts of Africa but it is totally inadequate in relation to the scale on which change is taking place and more research is needed into mixed communities in which livestock and wild herbivores co-exist (pp. 481, 507).

Cattle, sheep and goats now inhabit all vegetation types outside the tse-tse belt (see maps in Vol. I, p. 108 and p. 53 this volume) and are an important factor in the biology of many wild* species, modifying pasture, disease, numbers and even activity patterns.

If choice of the bovid family for domestication has its biological rationale in their superior digestion and physical hardiness, the choice of actual types owed more to the very limited range of species that was available in the Middle East between eight and ten thousand years ago. The origins of their domestication are therefore rooted in the faunal poverty of another continent and it is one of the paradoxes of the situation that the richest bovid fauna in the world is under threat from three species that could not last one year under natural conditions were they not assisted by a shrewd but exceptionally short-sighted primate. If we are ever to understand the processes that have shaped our environment and its inhabitants we shall have to know much more than we do about those major consumers of the vegetation—bovids. If we are ever to understand our own prehistory we shall have to devote much more attention to these, the prey of our ancestors.

How did this extraordinary variety of antelopes come into being?

One of the first points to consider is the early bovids' ecological niche and the nature of its initial adaptive advantage. It has often been assumed that the advantage lay in an ability to digest cellulose, particularly grass, but Hofmann (1973) has undermined this simplistic physiological explanation by showing that species from several lineages, particularly the more conservative ones, are actually unable to digest fibre. Young (1962) considered that rapid storage of food in the rumen allowed early artiodactyls to retire and digest in security, a pattern that is well exemplified by the chevrotain (Vol. IIIC, p. 300) and by smaller sedentary bovids which have well-known home ranges or territories. There can be little doubt that such species reduce their vulnerability to predators in this way but Hofmann (1973) has also stressed the saving in energy expenditure for a primitive ruminant that can quietly digest relatively large quantities of vegetable food in a safe refuge. An extreme example of a parallel ecological strategy is provided by the contemporary hippopotamus (Vol. IIIB, pp. 250—261).

Possible physiological advantages will be discussed shortly but the "security strategy" not only accords with the biology of several conservative artiodactyls but also helps to explain a number of unanswered questions, not least of which is the prolonged absence of bovids from the fossil record. Theoretically the longer history of conservative taxons should offer them a better chance of turning up as fossils, yet it is precisely types such as the neotragines and smaller tragelaphines that are rarest or wholly absent, for the simple reason that essentially solitary animals dependent on moist habitats for food and cover are the most unlikely candidates for fossilization. Instead it is the more recently evolved, larger, social, grass-eating species that are abundant as fossils.

Efforts at reconstructing the phylogenetic history and relationships of the bovids on the basis of these latter-day fossils have had limited success because the palaeontological samples are less representative of the bovid spectrum as a whole than the surviving fauna itself.

Sharpe's grysbok, *Raphicerus sharpei*.





Yellow-backed duiker,
Cephalophus sylvicultor.

For hiding and tranquil rumination to be wholly effective a solitary or near-solitary existence would have been essential and this is consistent with the social organization of all conservative bovids as well as primitive deer and chevrotains. Efficient spacing out of individuals according to the carrying capacity of the habitat would have depended upon mechanisms such as territorial marking, fights and displays. This may help to explain the early development of glands and short, spiked horns. However, solitariness would also have inhibited socialization, it is therefore significant that a high proportion of contemporary bovid species are solitary or near-solitary.

Palaeontological evidence for increasing sociality need not lie only in mass fossilization. As is discussed later, the elaboration of horns has a direct relationship with increasing density and with increasing body size, and these two parameters are dependent upon an expansion in the resource base, which usually involves loosening exclusive, year-long ties to a single patch of ground.

The paraphernalia and behaviour associated with exclusive territorialism show great persistence, albeit in peculiar distorted forms, even in very advanced, mobile types such as the alcelaphines, and this very conservatism is some measure of the long prehistory of organized solitariness that antedates the bovids' eventual socialization.

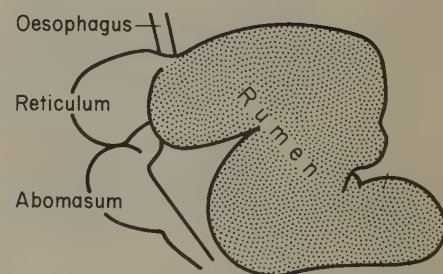
If Simpson (1945) and Romer (1945) correctly dated the parting of higher pecoran ruminants from the tragulines to the Eocene or early Oligocene, there is an undocumented run-up period of some ten million years before fossil bovids appear; during which time the Bovidae and their immediate ancestors were cryptic, inconspicuous and probably relatively small.

A major structural advance made by the pecorans over the Tragulidae in their digestive system has been the development of an omasum and the associated orifice between reticulum and omasum, a structure that helps to sieve food and slow down its passage and is concerned with absorption of water, inorganic compounds and volatile fatty acids (Campling, 1970; Langer, 1974).

Hofmann (1968) has remarked that the coiled "S" shape of the traguline type of rumen corresponds to the original arrangement of the ruminant stomach, and he has pointed out (Hofmann, 1973) that the evolutionary transformation of the stomach was a prerequisite for its association with a symbiotic microflora. Improving the chemical environment of the microflora might have been a major factor favouring further separation of the less acid fore-stomach from the strongly acidic hind-stomach. Rumination and fermentation of plant foods is found not only in artiodactyls but in several other mammal taxa, but protein breakdown and cycling of urea in the bovid fore-stomach is particularly advanced.

Barnard (1969) has demonstrated that one of the most important features of ruminant digestion lies in the efficiency of their nucleic acid/nitrogen metabolism which operates through copious pancreatic ribonuclease degrading RNA into assimilable form. This pancreatic enzyme processes RNA released by the death of rumen bacteria after they enter the fourth chamber of the stomach. A large part of the protein in the herbivores' food is taken up by these bacteria in the first place, and Nagy (1970) remarked that feeding a ruminant is really feeding millions of micro-organisms.

Janis (1976) considered that nitrogen cycling might well have been the initial adaptation of ruminants, she has pointed out that after being very largely fermented to ammonia, dietary protein is either used directly by bacteria or is absorbed through the rumen wall and sent to the liver, where the ammonia is converted to urea and then returned to the rumen, by inclusion in the parotid saliva or by diffusion through the rumen wall. This urea is incorporated into the actively reproducing bacteria, which then pass on to be digested by proteases in the abomasum where the nitrogen finally becomes assimilable as protein. Instead of being excreted in the urine, metabolic urea is fed into a cycle which uses all available nitrogen and, since water is needed for urine, Schaller (1967) has suggested that the process may also help ruminants to conserve water. Moir (1968) considered that the nitrogen cycle also protects the animal from amino acid imbalance in the diet because the rumen bacteria can synthesize all the animal's needs from limited original resources.



"S"-shape of rumen.
(After Hofmann, 1973.)

Sharpe's grysbok, *Raphicerus sharpei*.



It is difficult to imagine rumination developing in an active animal that was forced to make frequent other demands on its metabolism, so that the solitary "security strategy" could have been a behavioural prerequisite for the development of efficient rumination. It could also have meant that more active herbivores with fewer ecological constraints were dominant while the pecoran ruminants served their long apprenticeship in an ecologically restricted niche.

Numerous primitive ruminant types (some of them of localized distribution and relatively short-lived in the geological time scale) are known to have preceded the emergence of bovids. Bovid and cervoid may have

briefly shared a common root possessing the common adaptive advantage of a digestive system that had improved on that of the traguloids and made even more substantial advances on that of the tylopods.

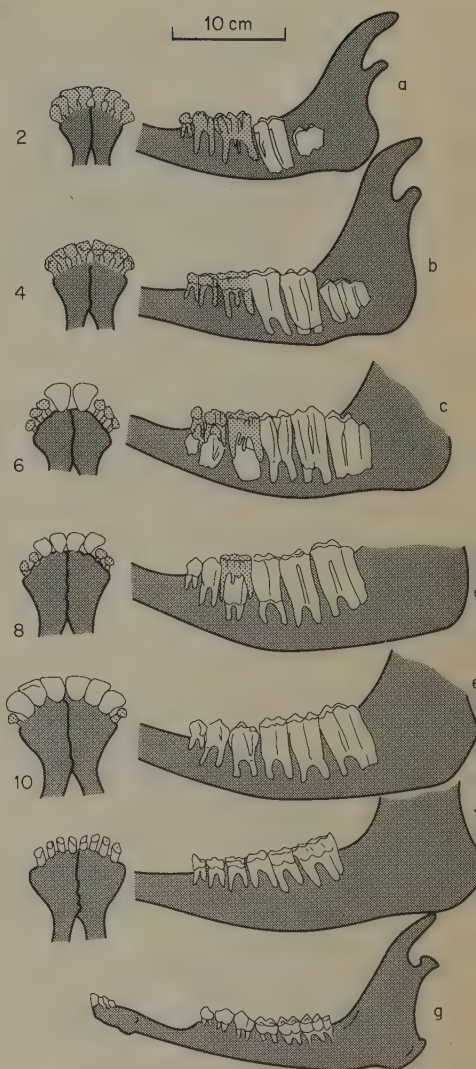
What lay behind the divergence between cervids and bovids? Although climatic boundaries between the two families are blurred in contemporary species, the overall pattern suggests that they originally aligned themselves along the extremities of a geographic and temperature gradient. Eurasian cervoids making an early accommodation to the seasonality and cold of upper latitudes while various degrees of resistance to heat may have been a major advance for early bovids. Acquired in Eurasia, such an adaptation could have assisted the bovids' early immigration into Africa and inhibited that of the cervids, particularly if there was any sort of drought belt separating the two continental masses. Thomas (1979b) has suggested that forests began to open up as late as 15 million years ago but Kortland (1980) has resuscitated much fossil evidence for relatively dry conditions in Egypt as early as the Oligocene.

A re-examination of the primary adaptive characteristics of early bovids is a necessary preamble to discussing their evolution, because the immense undocumented gap that precedes their first appearance as fossils begs some explanation.

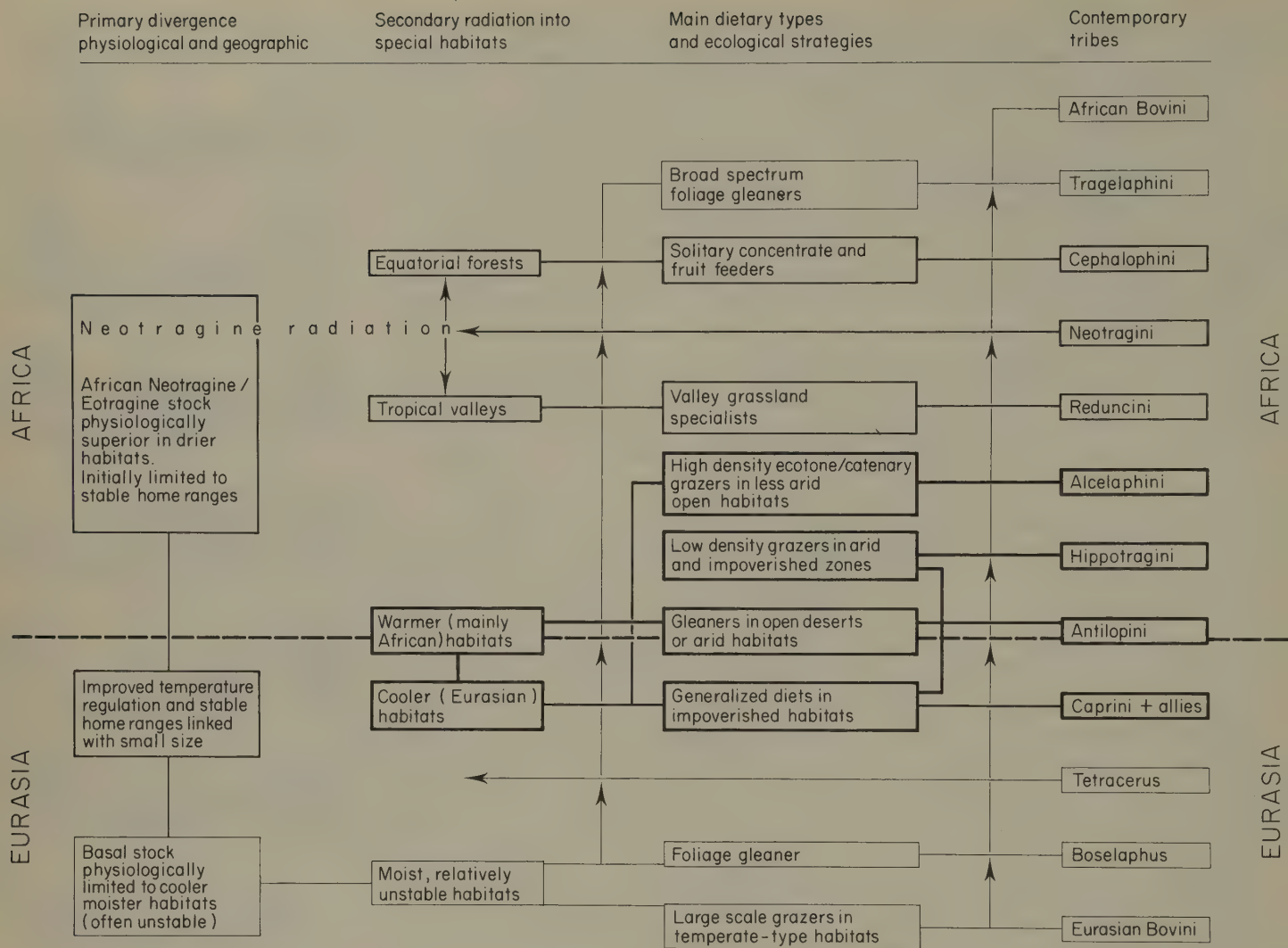
On present evidence their palaeontological debut comes long after their splitting into two main lines and the subsequent radiation of these into several distinct lineages. It is important for an understanding of modern bovid communities to recognize that the ability to digest cellulose developed independently in several of these branches and led to considerable parallelism in diet, body size and tooth structure. This late adaptation helps to explain the independent evolution of hypsodont dentition and appropriate digestive systems in several bovid tribes.

In North America fossil grasses became very abundant in Mid-Miocene deposits where equids and lagomorphs were dominant herbivores. It was the splendid sequence of American fossil horses that first demonstrated that complications of dental patterns and lengthening of teeth, hypsodonty, could be correlated with the adoption of a grass diet (Simpson, 1951). In Africa, antecedents of the grass-eating antelopes had almost certainly begun to differentiate on the basis of other biotic parameters *before* the major expansion of grasslands.

In the Ethiopian biotic region hypsodont bovids first appear in numbers at Al Jadida, a deposit about 13 million years old (Thomas, 1979b), whereas the Fort Ternan bovids, about one million years earlier, do not include hypsodont species. While this has some correspondence with a general expansion of grasslands at about that period (see pp. 10, 11) there is also likely to be a strong locality bias. Even today bovid species sampled from woodland localities are likely to include relatively few hypsodont grazers. As the habitat distribution chart (p. 21) shows, there remains a strong overall preponderance of folivores and frugivores in modern African faunas, even after allowance for the proliferation of duiker species (which are often highly localized and allopatric). Of the 48 bovid species recorded from East Africa there are nearly twice as many "concentrate selectors" (26) as grazers (15), seven species have mixed diets. While opportunities for diversification may



Buffalo mandibles (after Grimsdell, 1969): a. 9 months; b. 18 months; c. 2½ years; d. 3½ years; e. almost mature dentition (over 4½ years); f. very old buffalo; g. bushbuck for comparison with e. Note low crowns in bushbuck and hypsodonty in buffalo.

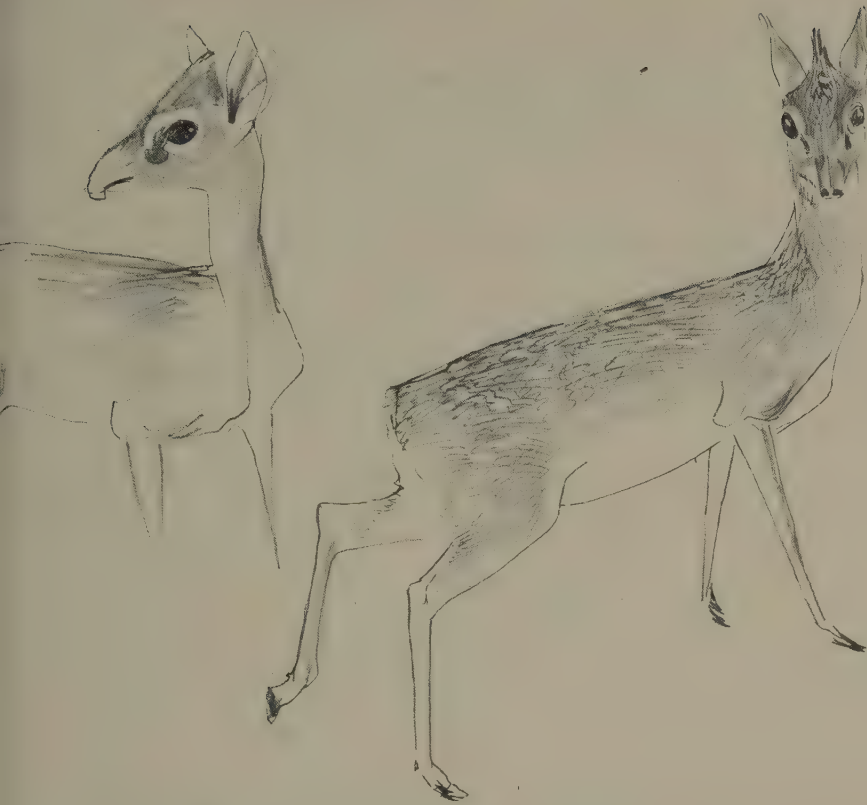


Diversification of the Bovidae in terms of some major physiological, dietary, environmental and geographic factors.

be fewer for grazers, I consider that this preponderance also reflects a much longer history of folivory and frugivory compared to grass-eating.

The provisional reconstruction of bovid radiation that is presented here has been pieced together from a variety of sources but an interpretation of form and function in the adaptive morphology of living antelopes has been an important guide to this arrangement.

There are at least six major adaptive trends in the Bovidae (col. 2, above) and, at the grossest level of generalization, there are six lineages, each with well-defined ecological preferences. The most significant adaptations probably concern their feeding habits and physiology. In each of these lineages there is a size gradient in which the most primitive, and sometimes the most specialized, species tend to be smaller and the more advanced types larger. The range of sizes varies enormously, with the largest duiker being about 80 kg and the buffalo 800 kg. Likewise the smallest bovine (an Asiatic island buffalo) is about 150 kg, the smallest duiker about 5 kg.



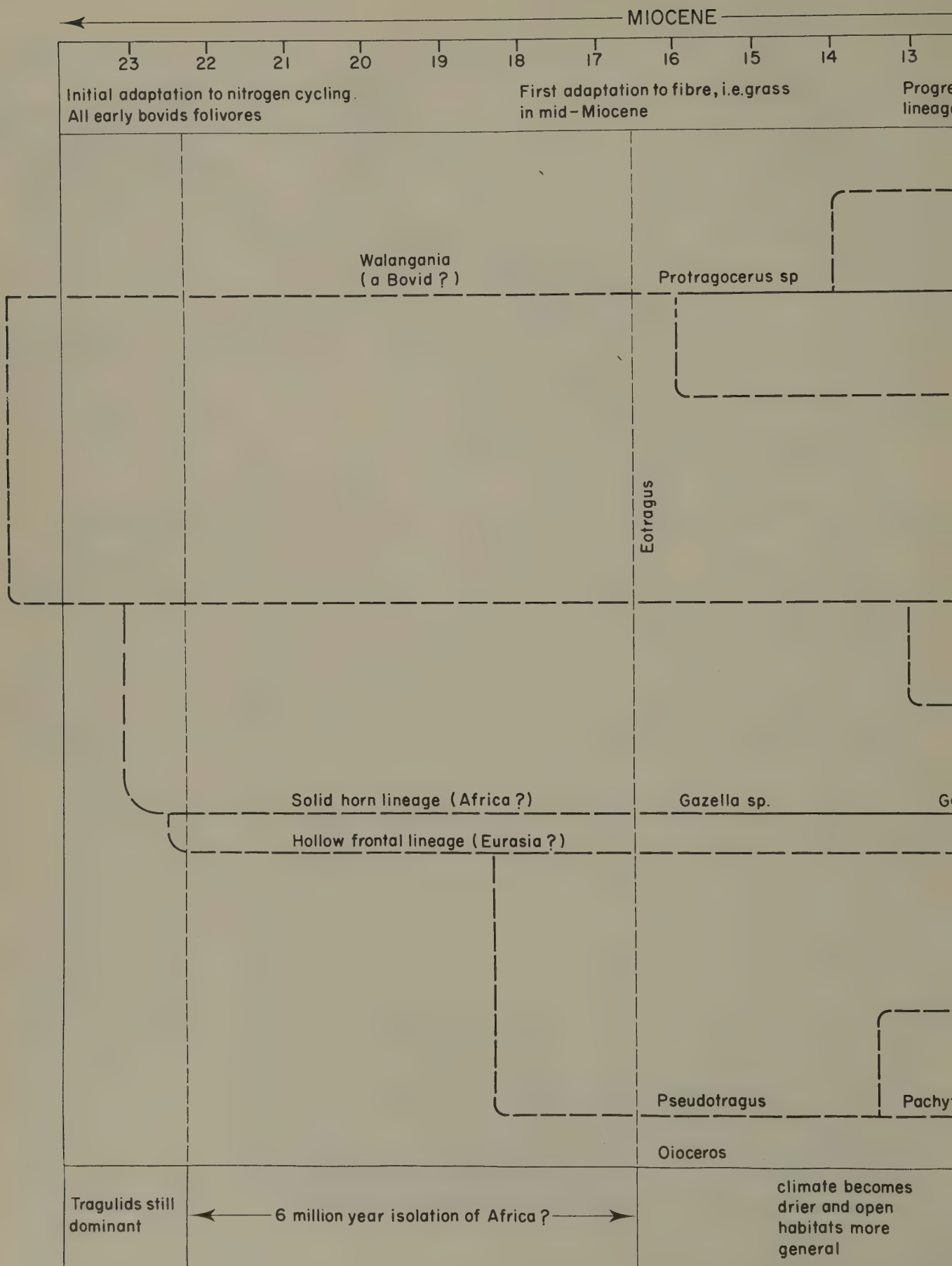
Left: dik-dik, *Madoqua guentheri*.

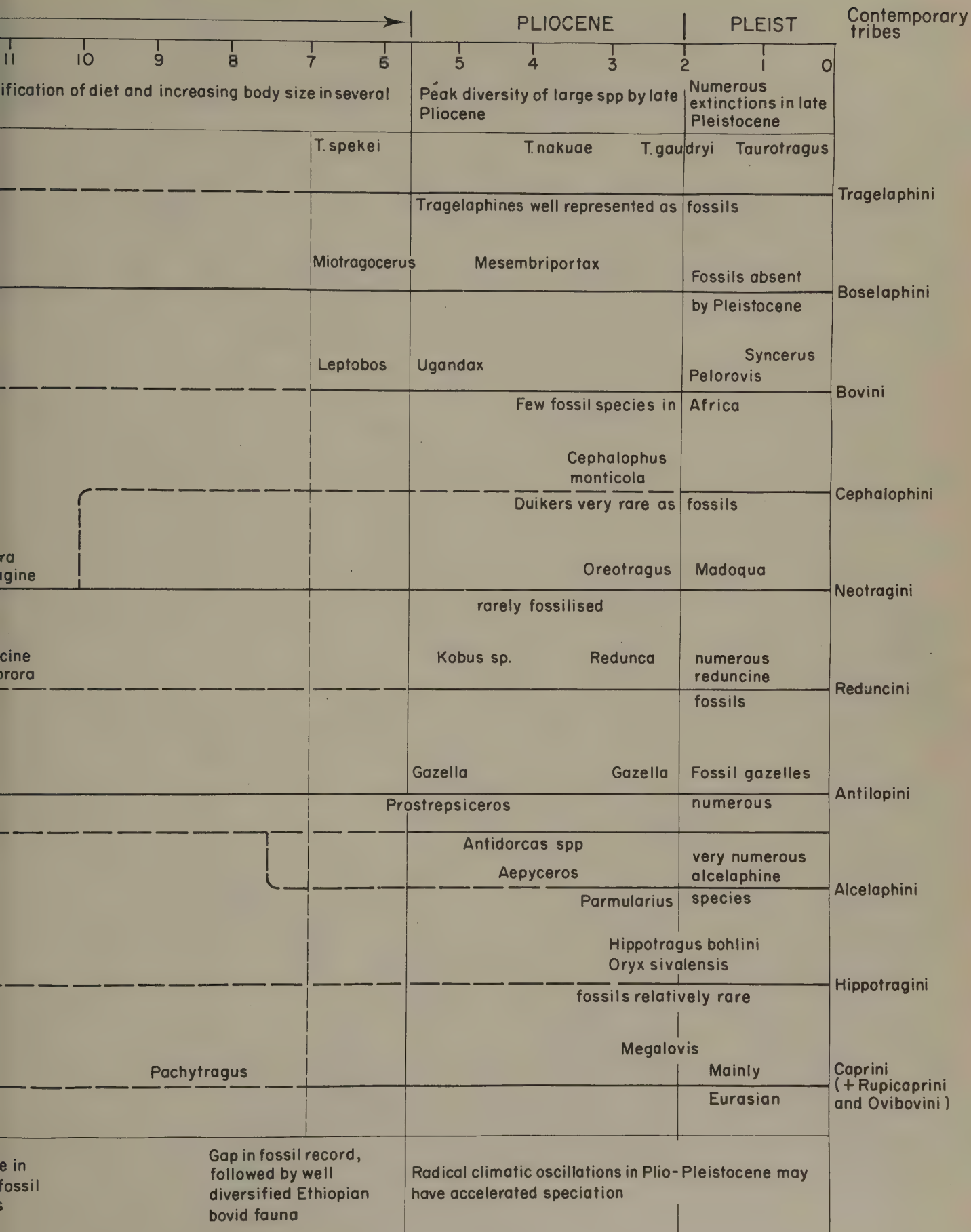
Above: buffalo, *Syncerus caffer*.

Size ranges can be related to at least three major factors: the relative age of the lineage, social structure and diet. Duikers with a scattered food supply and spaced out territorial systems appear to have originated relatively recently from a diminutive ancestor. Bovini and Tragelaphini (with all the big heavy-weights) have hierarchies and the buffalo is a bulk grazer. Both derive from an ancient Asiatic root stock. The Asiatic origins of Bovini and Tragelaphini are shared with *Boselaphus*, a relic Indian antelope, which has given its name to the well-represented fossil group Boselaphini. There is general agreement as to the relatedness of these three groups and for the proximity of boselaphines to the main stem of bovid evolution (Gentry, 1978). The other antelopes can be distinguished by their annulated horns and the presence (or presence in ancestors) of fossae for facial glands. In the smaller species facial glands correlate with sedentary territorialism, and a strongly territorial ancestry could have influenced the group's smaller body-size ranges relative to the Bovinae (see p. 18).

The development of facial glands and a system of labelling animals or their surroundings with oily secretions could have evolved in relation to hotter, drier environments. In moist habitats urine is available as a common mammalian vehicle for the detection of oestrus in females, for the advertisement of dominance in males and for evidence of an animal's presence.

In drier habitats water economy may impair the usefulness of urine and rapid evaporation limit its effectiveness as a signal. An animal can transmit information about itself, including its sexual condition by means of aromatic apocrine or sebaceous secretions and these have the virtue of being economic, pungent and lasting, particularly in a warm, dry climate.





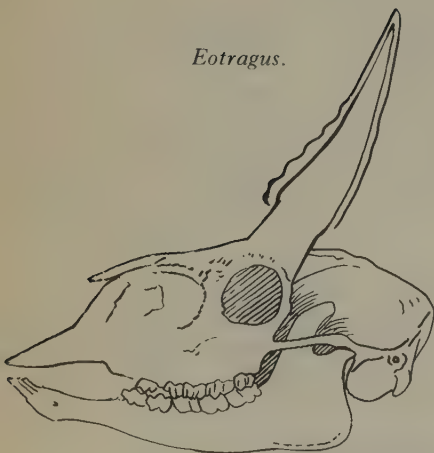
The more immediately obvious differences between the two branches can be summarized in tabular form.

	BOVINAE	ANTILOPINAE
<i>Horn type</i>	Smooth, circular in section or spiral twist	Short and smooth in small conservative spp. Mostly annulated, very variable in shape
<i>Thermo-regulation</i>	Sweating	Nasal panting (sweating in some Reduncini)
<i>Pedal glands</i>	Always absent	Present or absent
<i>Mammæ</i>	Two pairs	One or two pairs

At some time near the Oligocene/Miocene boundary the Antilopinae seem to have become distinct from the main boselaphine/bovine lineage. It is possible that the initial parting lay in a continental separation of populations. If this was so, it is likely that all the antelopes with annulated horns (which are classified as Antilopinae in this work), had their earliest origins in Africa. A major factor of their divergence may have been temperature regulation which is achieved by different means in the two divisions.

Taylor (1972) investigating evaporative water loss in antelopes found that representative alcelaphine, antilopine and hippotragine species were "panthers" whereas the tragelaphine eland lost most of its water by sweating. He recorded the waterbuck as a "sweater" but this is probably a secondary development. Johnson (1977) reported that the zebu, a tropical representative of the Bovinae has very abundant sweat glands (about 1,600 per sq. cm). To regulate body temperature by sweating requires frequent drinking and a fairly large body surface. Smaller animals cannot afford to lose the same amount of moisture and they must use a more economic method of evaporative cooling. This has developed in the Antilopinae in the form of nasal panting (see p. 249). While size differences alone could have initiated this development, it had the very important effect of allowing smaller bovids to invade drier habitats. The evolutionary picture presented here is consistent with an initial colonization of Africa by fairly small dry-country antelopes. Their modified living representatives are the Neotragini, a group whose fragile little bones have yet to turn up in early fossil beds.

There are in Eurasia and Africa Mid-Miocene fossils of a spike-horned antelope with primitive teeth and skull and large fossae for facial glands which provide some indication of the ancestry of this sub-family. This species, *Eotragus*, was too large and too late to be an actual ancestor. Furthermore it had well-developed horns and it co-existed with gazelles and caprines which belong to later stages in the evolution of Antilopinae. Its generalized or primitive features, therefore, have to be projected back in time to envisage still earlier forms. Such extrapolation from later survivors can be augmented by reference to the Neotragini, and from this combination some sort of



Eotragus.



reconstruction can be made of the eotragine-cum-neotragine ancestry of the Antilopinae.

Of the seven or more tribes belonging to this major sub-family the neotragines, cephalophines and reduncines have unquestionable African origins and, in my view, the last two derived directly from a neotragine stock that was already well diversified.

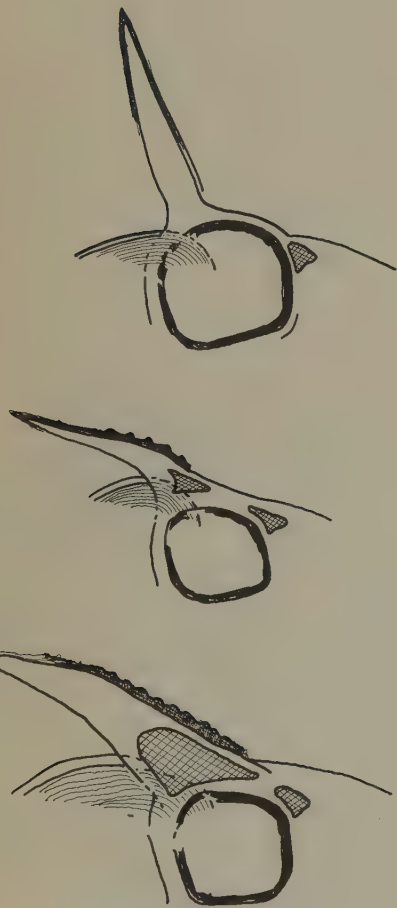
The Antilopini and their predominantly Eurasian relatives the Caprini (plus allied Rupicaprini and Ovibovini) would have been an earlier development out of the eotragine/neotragine basal stock. If the primary parting of Bovinae and Antilopinae was within Eurasia (an unlikely possibility) rather than between that continental mass and Africa, then the earlier caprine and gazelline antelopes could have hived off in Asia before the later developments in Africa. Further fossil finds may help to determine this point and it might justify splitting or further subgrouping of the Antilopinae (as defined in this work).

The very wide distribution of Antilopini and Caprini in hot desert areas today is one of the indications that a significant innovation of their common progenitor was adaptation to heat stress. This also explains the ready movement of gazelles across the relatively arid ecological barrier that is thought to have existed between Africa and Eurasia since the Mid-Miocene (Thomas, 1979a). It remains to be seen whether radiation of the caprine lineage took place in Eurasia after the return of primitive Antilopini from Africa, or whether they have a purely indigenous history. In either case it seems likely that the emergence of caprines followed a very early separation of primitive Antilopini into a gazelline type with solid horns emerging directly from the orbit and a second type which developed sinuses in the frontal bones. This early bifurcation of the "hollow frontal" antidorcines from more primitive gazellines could well have been geographic in origin, the former being the Eurasian offshoot of an earlier African branch.

There is a functional dimension in that the development of frontal sinuses probably had a direct relationship with intensified head-to-head butting and insulation of the brain. Several points can be made in this respect. Head-to-head contests have a correlation with larger body size and this in turn must serve to increase concussive force when heads meet in apposition. Slender backswept horns shield the brain less from direct compression during head clashes, and changes in the basi-cranial axis or reduction in the prominence of orbits (and hence the horn bases) can increase frontal exposure of the cranial capsule. Any of these conditions could have exerted selection in favour of an insulating mechanism. A cross-section of the backswept horn core and frontal of a dik-dik, *Madoqua*, (margin, p. 15) reveals minuscule diploe in the basal interior layer of the frontal. Similar air spaces could provide the basis for inflation to take place in primitive Antilopini.

Whereas mechanical considerations probably put upper size and weight limits on the horns of gazellines, separation of the frontals into inner cranial surfaces and an outer bed-plate for the horns eventually introduced new possibilities for the enlargement and elaboration of horns without detriment to orbits or brain.

Regardless whether the parting between gazelline and antidorcine types was along a geographical or an ecological boundary, temperature could have

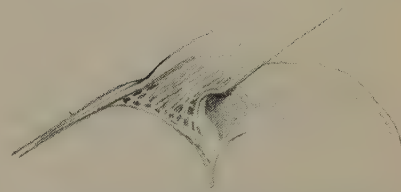


The development of hollow horn bases and frontal bones. Top: neotragine; bottom: caprine or alcelaphine type of hollow horn; middle: hypothetical early development in species with a backwardly deflected and corrugated horn and exposed brain case.

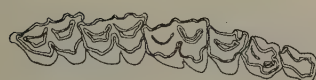
been a significant parameter in either case. Furthermore, their divergence to be maintained was likely to have been associated with dietary differences. It is surely no coincidence that the two African and the three Eurasian tribes that seem to have antidorcine ancestry are predominantly grazers, particularly in the larger size ranges. The physiological basis for processing this difficult diet (notably increasing cellulolytic bacteria), is likely to have been anticipated by ancestors with foods that were more fibrous than those of their gazelline relatives.

A more abundant food resource allows larger size and greater numbers, the ephemeral nature of grass demands movement, which also favours larger size and the abandonment of fixed home ranges. It is not surprising therefore that phylogenetic increases in body sizes are especially characteristic of grazing lineages.

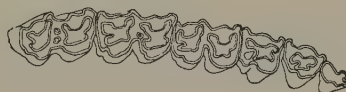
A most important point to be made here is that increased body size may transform even those features that are most commonly used for classification and the assessment of affinities—the teeth.



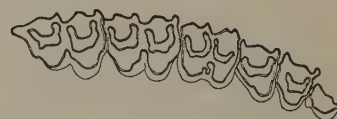
Horn core section of a dik-dik, *Madoqua*.



a gazelle



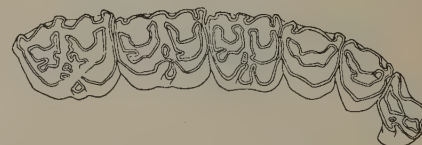
b hartebeest



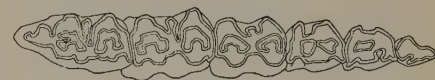
c waterbuck

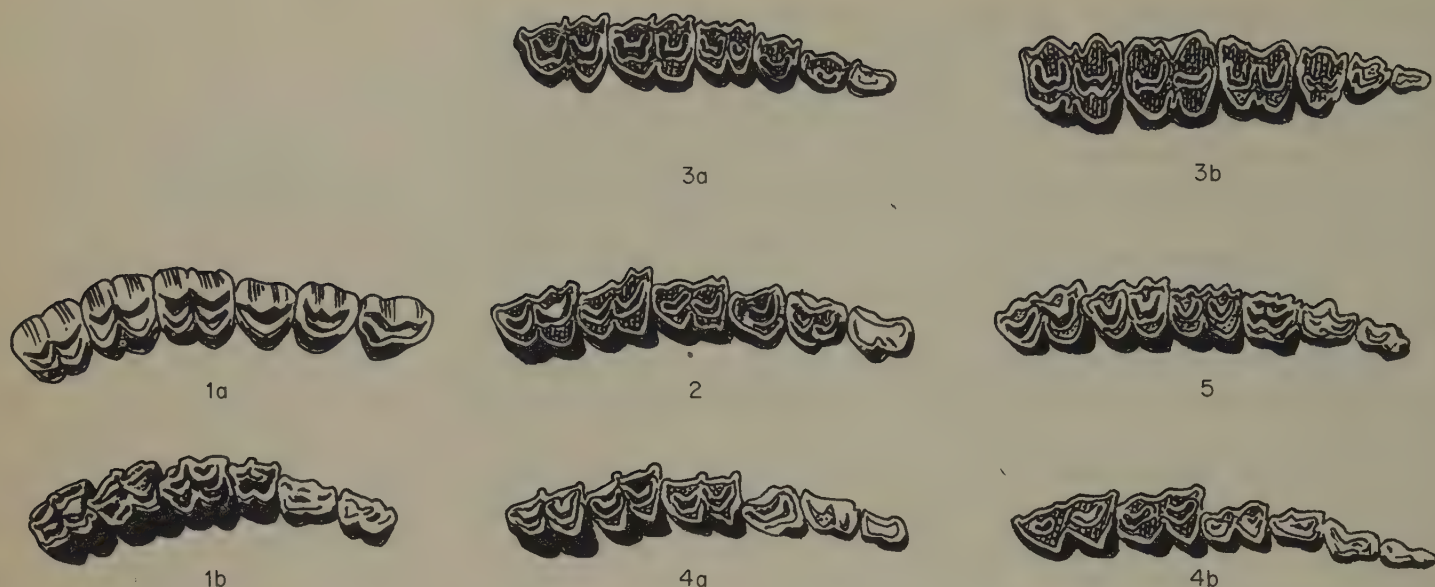


In bovid phylogeny this has wide-ranging implications, Schlosser (1903) was the first to attempt a classification of the Bovinae according to their dentition. He broke down the wide variety of types with all their peculiarities and gradations into two major categories: the Boodonta (with less hypsodont teeth, pronounced basal pillars, greater persistence of molar lobes, shallower mandibles and a long premolar row and the Aegodonta (with hypsodont teeth, fusion between the molar lobes, short premolar rows and a deeper mandible). These may be useful descriptive terms but, as Simpson (1945) remarked, the dichotomy is oversimplified and produces unnatural collocations when applied to taxonomy or phylogeny. Classification by the structure of the teeth produces unnatural groupings because the teeth of different lineages have responded to tougher diets and larger body size in very similar ways. Thus the Hippotragini, the Alcelaphini and the Reduncini are all antelopes that belong to the large-sized, advanced section of very different adaptive types. They have been quite unnaturally clumped by some taxonomists on the basis of superficial similarities in tooth structure. In fact, dentition is the last thing that should be considered in tracing bovid relationships because there are otherwise conservative species which have altered little else but their teeth.



d buffalo





Occlusal views of the upper right toothrows in 1a. *Eotragus clavata*, and 1b. *Eotragus sansaniensis*. *Eotragus* is currently thought to be the most primitive known bovid; 2. *Raphicerus melanotis*, the most generalised of neotragines; 3a. *Ourebia*, the only grazing neotragine; 3b. a specialised grazer, *Redunca fulvorufula*; 4a. *Neotragus moschatus* a concentrate selector; 4b. *Neotragus batesi*, a strict folivore; 5. *Cephalophus adersi*, predominantly a frugivore.

The nature of dental modification in relation to diet is well exemplified by some neotragine and cephalophine species, where complicating factors such as size differences are less extreme.

The most generalized tooththrow is found in the grysboks, particularly *Raphicerus melanotis* (Fig. 2), a formation not dissimilar to that of the larger sized Miocene fossil *Eotragus* (Figs 1a, 1b).

In the oribi, *Ourebia*, which is a grazer, the molars have broadened and deepened and the premolars are reduced in size and functional importance (Fig. 3a). Increased hypsodonty in the oribi's molars not only involves elongation of the enamel covered cusps but milling edges across the molar face have been multiplied by folding of the enamel surfaces that is made possible by widening of the dentine-filled spaces between these crenellated layers of enamel. Teeth of the related Reduncini carry this modification further with thicker dentine and extra folding, especially on the inner lingual surfaces of the tooth (Fig. 3b). The combination of extra folds or accessory buds and pillars and more soft dentine packing in between the enamel ridges improves the milling action of mastication, while it reduces the slicing component because the lingual indentations between cusps and between individual teeth get filled in, reducing thereby the interdigitation of sharp cusp blades in the upper and lower toothrows. The front end of the tooththrow loses its importance because the length of fore-aft tooth surface that can mill fibre efficiently under a side-to-side or lateral mode of mastication is very limited and needs to be concentrated in the area where buttressing of the teeth and mechanical advantage in the action are optimal. The

mechanism for achieving hypsodonty is not materially different in other bovid taxons, hence much similarity in the end products.

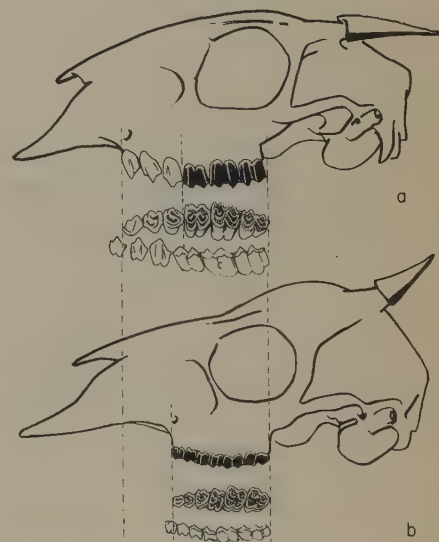
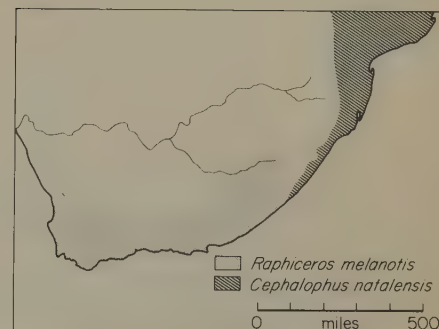
Where the masticatory action of the toothrow is to slice rather than mill, the premolars retain their importance and this is evident in the narrow rows of the folivorous *Neotragus* (Fig. 4a). In particular the equatorial forest species, *Neotragus batesi*, is an exclusive folivore (probably because a highly diversified duiker community has pre-empted any other diet). Leaf-eating has become so specialized in this species that the toothrows in both upper and lower jaws have narrowed to long saw-edged blades (Fig. 4b).

In this connexion it is possible that the retention of a generalized dentition in *Raphicerus melanotis* (and its restricted distribution) are linked with the absence of red duikers in the Cape.

The dentition of many *Cephalophus* species is generally conservative in morphology (Fig. 5) but the tooththrow of one species, *C. monticola*, is very suggestive of the secondary enlargement that I consider has taken place in the Cephalophini (see p. 264). The length of the tooththrow in this species is no greater than in *Neotragus batesi*, yet the overall dimensions of the rest of the skull are substantially larger (see p. 266). The implication is that the teeth failed to enlarge longitudinally at the same rate as skeletal and other features, but molars and premolars in both upper and lower jaws have made some lateral expansion. Instead of the premolars being well-differentiated in function or semi-redundant, as they are in many other bovids, the entire pygmoid tooththrow has been retained but expanded in *C. monticola* to form a single, compact and well-buttressed set of grinders. If the proportions of the skull in this species are compared with those of *C. dorsalis*, a larger duiker with strongly differentiated premolars and molars (see illustration), it can be seen that the "molar zone" in *C. dorsalis* approximates to the entire tooththrow in *C. monticola*. The latter tooththrow probably performs a single masticatory action instead of having the two distinct components which I have observed in *C. dorsalis* (p. 316).

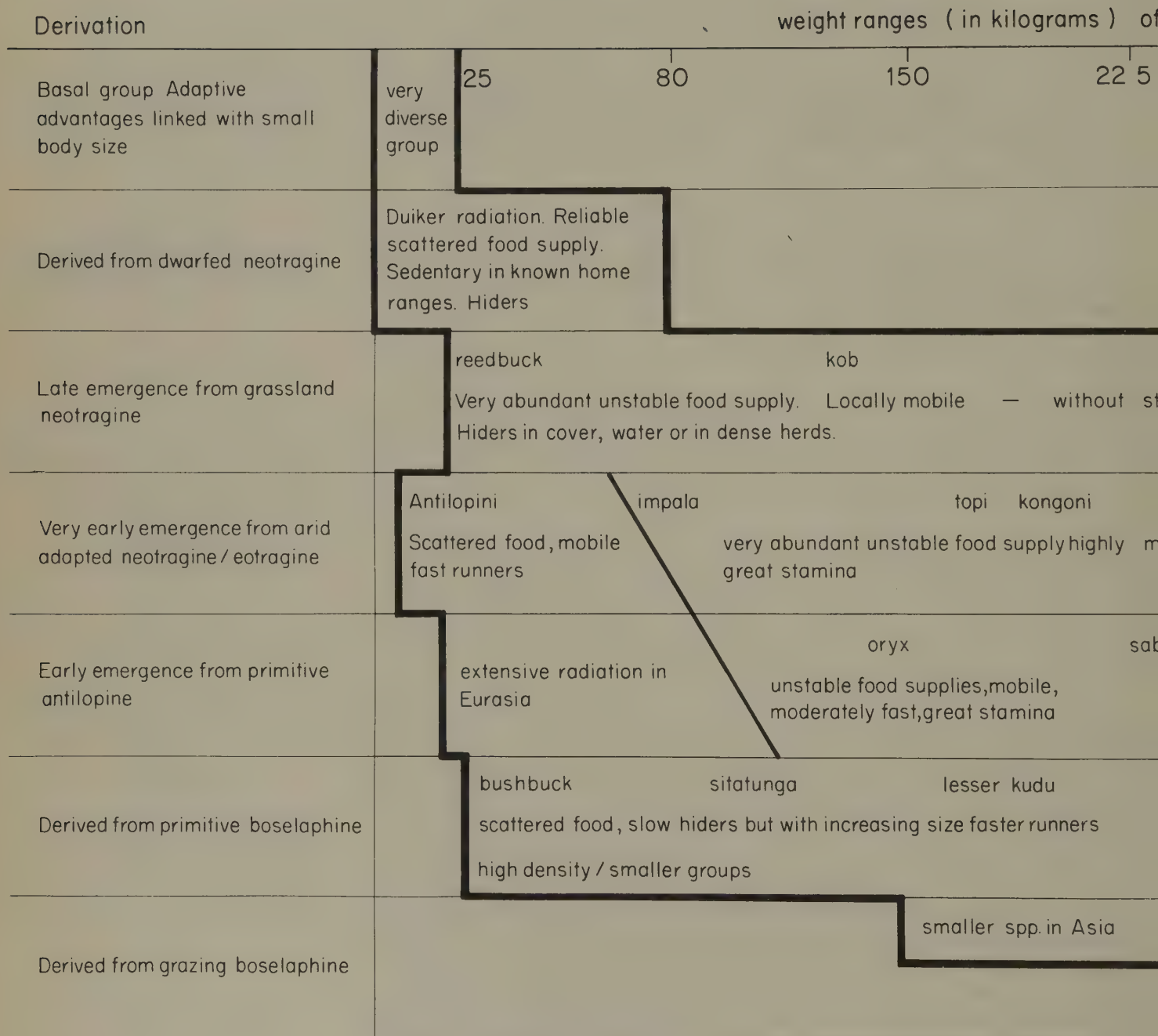
The tooththrows of *Cephalophus* illustrated on this and the preceeding page show that dentition is subject to considerable modification in spite of the genus being strikingly uniform with respect to body build and overall biology. This dental plasticity is general in the family but is particularly well illustrated by the Cephalophini and Neotragini.

Bovid teeth are evidently highly responsive to diet and probably to the mechanical alterations that must accompany allometric changes in skull proportions. One must conclude, therefore, that dentition divorced from its adaptive function is an unsuitable criterion for bovid taxonomy and that much of the long-standing confusion can be traced to a misplaced reliance on teeth. The simplified dendograms on pp. 8 and 10 summarize my conception of bovid evolution. On p. 8 geographic, climatic and physiological dimensions are suggested for the first bifurcation between ancestral Bovinae and Antilopinae. Larger sized Eurasian boselaphines adapted to moister habitats, smaller African eotragine/neotragines adapted to drier habitats. Splitting within these two basal stocks is portrayed in a conveniently simplified form as a secondary adaptation to specialized habitats. The dominant African antelopes having become larger and longer-legged, either remain as "gazelles" or branch into Asia as the pre-caprine or antidorcine



Comparison of skull proportions in relation to the tooth row in a. *Cephalophus dorsalis* and b. *Cephalophus monticola*.

ECOLOGICAL



NICHES OF BOVIDS

Lineage and feeding strategy			
300	500	750	1000
Neotragini. Conservative, size-limited radiation			
Cephalophini. Forest concentrate selectors			
waterbuck	Reduncini. Valley grazers		
	Antilopini. Arid land gleaners / Alcelaphini. High density ecotone / catenary grazers		
roan	Caprini. Asiatic specialists / Hippotragini. Low density and arid adapted grazers		
bongo	eland	Tragelaphini. Foliage gleaners	
low density / larger groups			
African buffalo	Bovini. Fresh grass bulk grazers		
Abundant food in rel. unstable habitats large mobile herds, slow gait			

branch of the Antilopini. Two other African radiations, one into the forests the other into valley grasslands are indicated (without any implication of synchrony). Arguments for the subsequent arrangement of proliferating groups are scattered throughout the text of this volume, but diet, habitat and dispersion patterns provide clues to the niches occupied by contemporary bovid tribes. In the second dendrogram on p. 10 this schema is tentatively related to the fossil evidence.

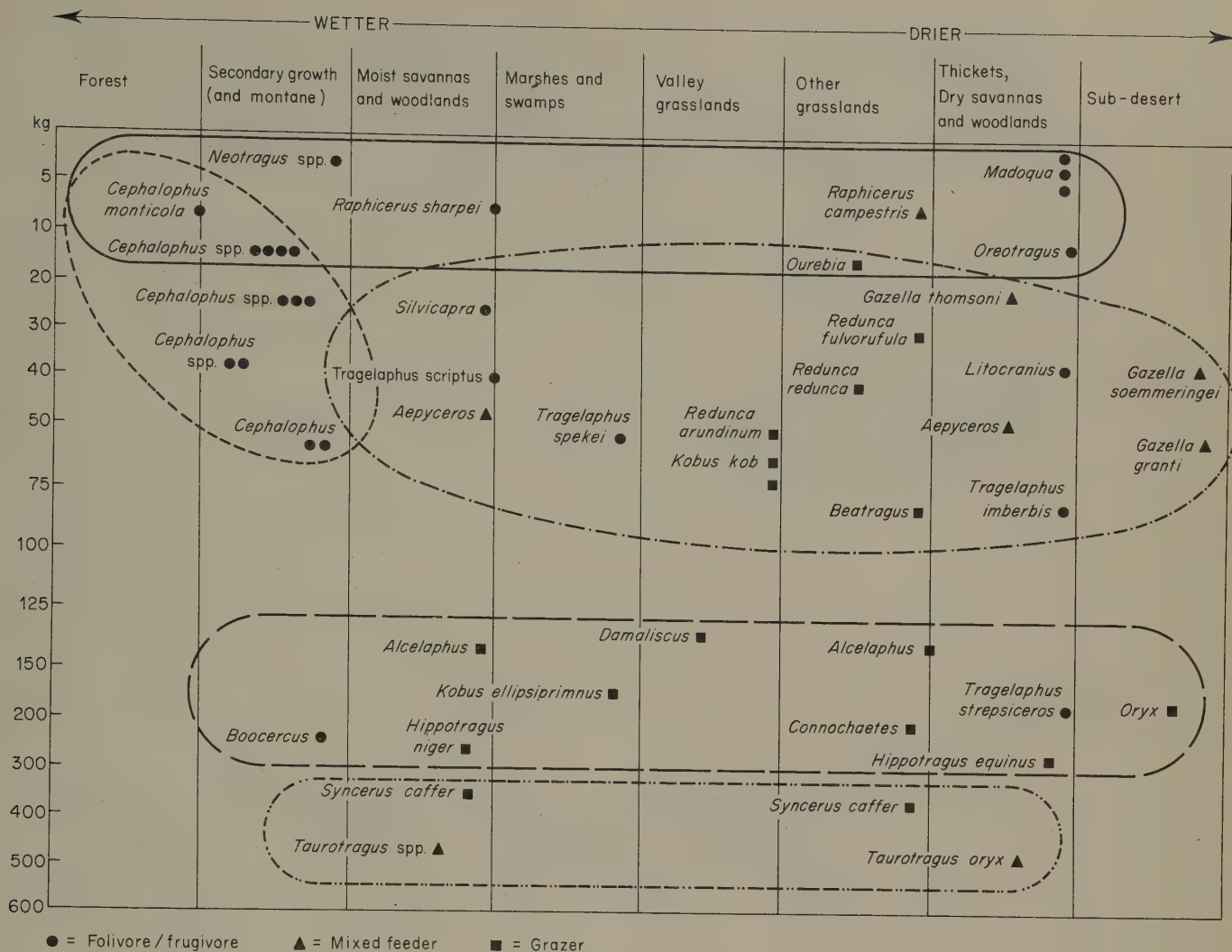
In the pages that follow, it is phylogenetic entities that are stressed, partly because the book is a systematic inventory of species, and partly to assert that ecological adaptation is not a surface feature but something at the very roots of bovid speciation and diversification. Diet and size have been emphasized because they are central not only to the delineation of species, their habitat and the details of their morphology but to understanding the broad sweep of their evolution. The chart opposite demonstrates that living antelopes are well-distributed through the available habitats. I have allocated the species to a simplified range of vegetation classes similar to those used for rodents (Vol. IB, pp. 366—367) and carnivores (Vol. IIIA, p. 405). Habitat distribution is plotted by body weight. The dietary categories follow Hofmann's (1973) definitions and symbols indicate which species are grazers, which are "concentrate selectors" (a pronounced majority) and which are mixed feeders.

The distribution of body weights reveals clustering and what appear to be well-marked thresholds in body size. For example, there is a conspicuous absence of species between the 75 and 150 kg size classes. Most of the antelopes between 25 and 75 kg have a rather generalized body build, although lengths of leg and neck vary considerably. In contrast, the species weighing over 150 kg show much greater morphological diversity, the most extensive transformations being in the Alcelaphini.

Another boundary lies at about 300 kg. The anatomical reorganizations needed to carry weights in excess of this are manifest in the compact proportions of buffalo and eland; the latter being in my view the phylogenetic transformation of a giant kudu (p. 79). (Sexual dimorphism in the bongo straddles this threshold, with interesting differences in the build of adult males and females.)

There is a less well-defined separation of the 25—75 kg antelopes (which tend to have straighter backs and more rectilinear stances) from those weighing between 5 and 15 kg, which have different gaits, arched backs and necklines. The cluster of species belonging to the latter class includes most of the Neotragini, a taxon that is based more upon size-linked resemblances than on a recent common heritage. Similarities between these antelopes and the other small-sized group, the duikers, are not fortuitous, as the latter appear to originate from neotragines that were still further dwarfed. Extreme diminution of body size might have initiated some of the distinctive features of duikers (p. 264) but, once acquired, duiker characteristics have remained remarkably constant up to body weights of over 80 kg.

There are some fundamental implications for the overall pattern of bovid evolution in the conclusion that forest-living and omnivorous-frugivorous diets in duikers are secondary developments (see p. 268). Had these been primary adaptations and the duikers a truly primitive group, the radiation



Simplified chart of habitat distribution of Bovidae according to size.

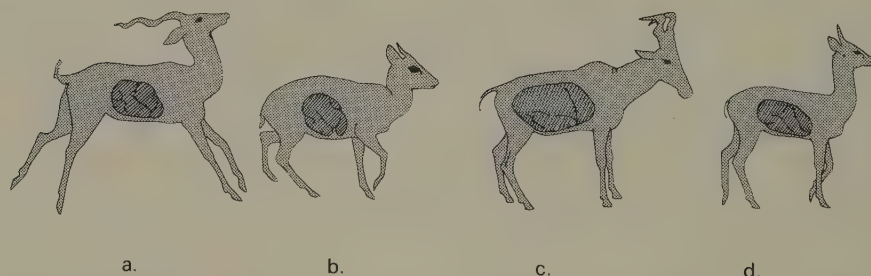
of African antelopes could be more readily portrayed as a gradual, progressive emergence of chevrotain-like animals out of the forest into more open habitats, as has been suggested by Estes (1974).

The duikers' secondary invasion means that the earliest African bovids were not forest forms and it confirms that the relatively omnivorous tragulids are much more distinct from the predominantly herbivorous bovids than should be allowed by Estes' more gradualist conception.

Antelopes are not the only mammal group to have invaded the African forests from more open milieux. I have suggested in earlier volumes that the tree hyraxes and guenons (*Cercopithecus*) derived from more terrestrial, less forest-adapted ancestors (Vol. I, pp. 141—146). Forest squirrels, (Vol. II, pp. 369—371, and Moore, 1959) and murids (Vol. IIB, pp. 502 and 570, and Misonne, 1969) all derive from Eurasian immigrants that have invaded the

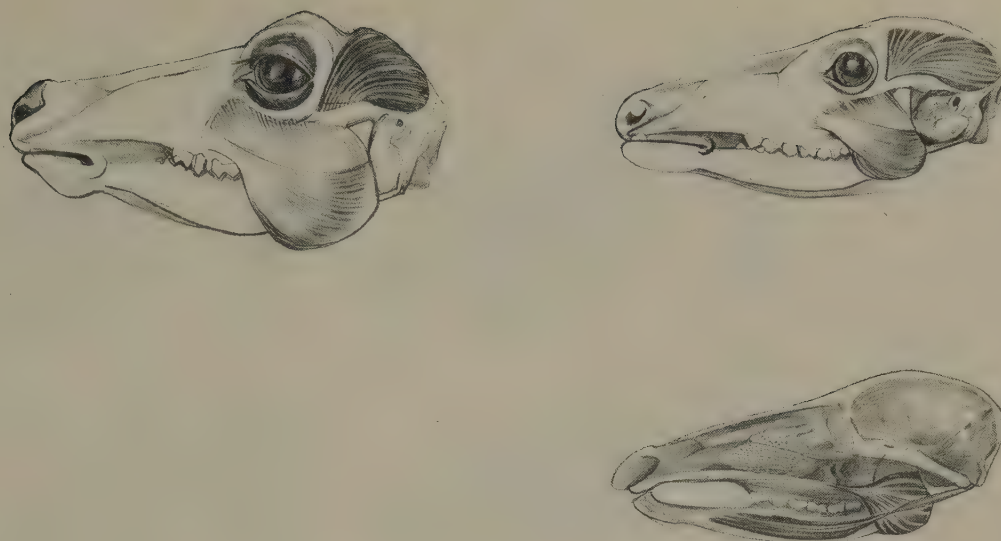
African forests from drier, less closed habitats. Bovidae together with Sciuridae, Muridae and *Cercopithecus* are the dominant frugivorous and herbivorous mammals of the African forests. Recognition that they are all invasive groups is of great importance for our understanding of evolution in Africa, hinting as it does at past climatic vicissitudes and the interaction of different herbivore and frugivore stocks (see Vol. I, pp. 62—7 and Vol. II, p. 371, and Kingdon, 1980; 1981).

There is a clear anatomical demarcation between neotragine antelopes and duikers and a similar break between the neotragines and reduncines, but there is one very significant animal which combines characteristics of the last two groups as well as having its own features (principally an extraordinary arsenal of olfactory devices). This species, the oribi, is at 18 kg the smallest grazing antelope. According to Kleiber (1961) the high metabolic rate of a small animal precludes a high fibre diet and the oribi should be below the optimum size for efficient cellulose digestion. Hoppe (1977a) has shown that cell-wall nutrients are only extractable after about 24 hours' fermentation (which should generate long-term storage problems in a small animal), whereas more soluble cell contents need as little as one hour of fermentation to release nutrients. Furthermore, rapid passage may be essential to concentrate selectors, because lactose-fermenting organisms could lower pH to levels intolerable for the stomach flora (Hofmann, 1973).



Ratio of stomach to body size as an indicator of concentrate or fibre in the diet: a. large selector (lesser kudu); b. small selector (suní); c. large grazer (hartebeest); d. small grazer (oribi). (After Hofmann, 1973.)

The need for larger stomach fills and long passage rates means that bigger animals are better able to digest grass. Nonetheless, the oribi and mountain reedbuck demonstrate that relatively small ruminants can survive on grass diets in favourable habitats, while the folivorous kudu and bongo show that, contrary to some fashionable assumptions, there is no fixed relationship between large size and grazing. The most striking visual demonstration of these contrasts is revealed by a comparison of relative stomach and body sizes in representative species (above). In a comparison of eleven East African ruminants, Hoppe (1977a) found a correlation between rumen fermentation rates and metabolic body weights, but he stressed that the larger species retain more than one option—they can slowly ferment a high-fibre diet in a capacious rumen (c) or they can rapidly ferment smaller quantities of richer more soluble dicots (a). Mixed feeders can find intermediate positions between these extremes depending on the pattern and level of resources in their habitat.

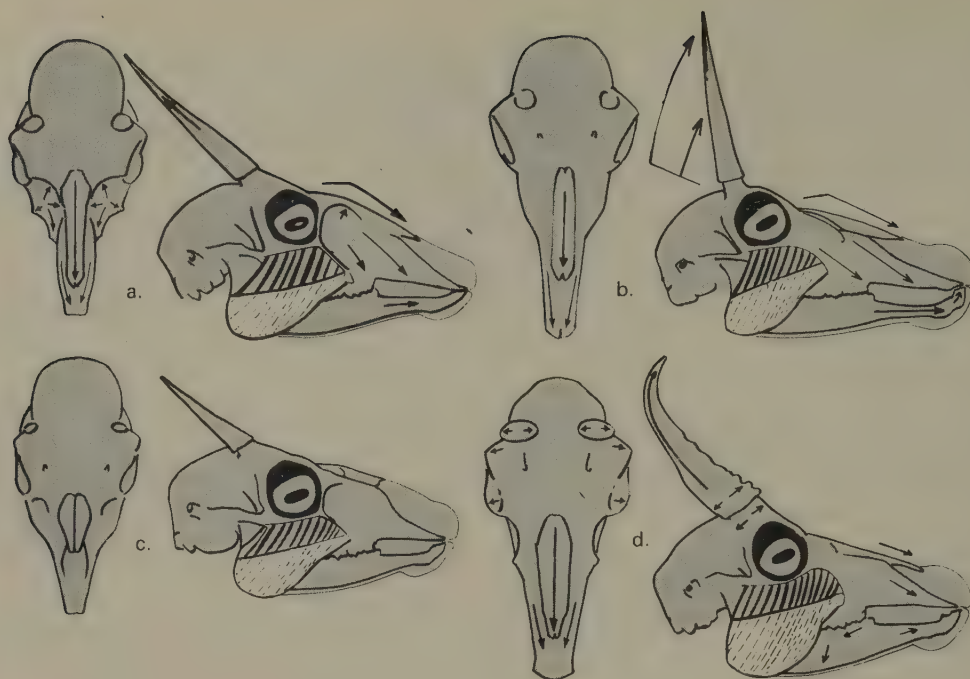


The proportions and angulation of masticatory muscles and mouth parts in grazing and folivorous antelopes. a. *Redunca fulvorufula*; b. *Tragelaphus scriptus*; c. mid-line section of b. to show pterygoid and digastric muscles.

Contrasts in relative stomach size can be matched by similar comparisons of the masticatory apparatus. At the grossest level a coarse grass grazer such as the mountain reedbuck, *Redunca fulvorufula*, can be compared with the bushbuck, *Tragelaphus scriptus*, a typical concentrate selector, even the most superficial dissections revealing enormous differences in proportions of the masseter, teeth and the surrounding bony structures (see above).

Such comparisons demonstrate a straightforward functional correlation between tough diet, robust, well-buttressed molar teeth, deeper, thicker masticatory muscles and extension of the bony areas to which they are attached. Of course these muscles have several parts and layers which are not immediately apparent in a superficial view (see sketches of oribi masseter and temporalis). The action of the two larger muscles is augmented by pterygoid and digastric muscles inside the jaws (see lower head, above), but the external dimensions and angulation of the masseter alone have an excellent correlation with diet and have an obvious role in determining the exact shape of an antelope's head.

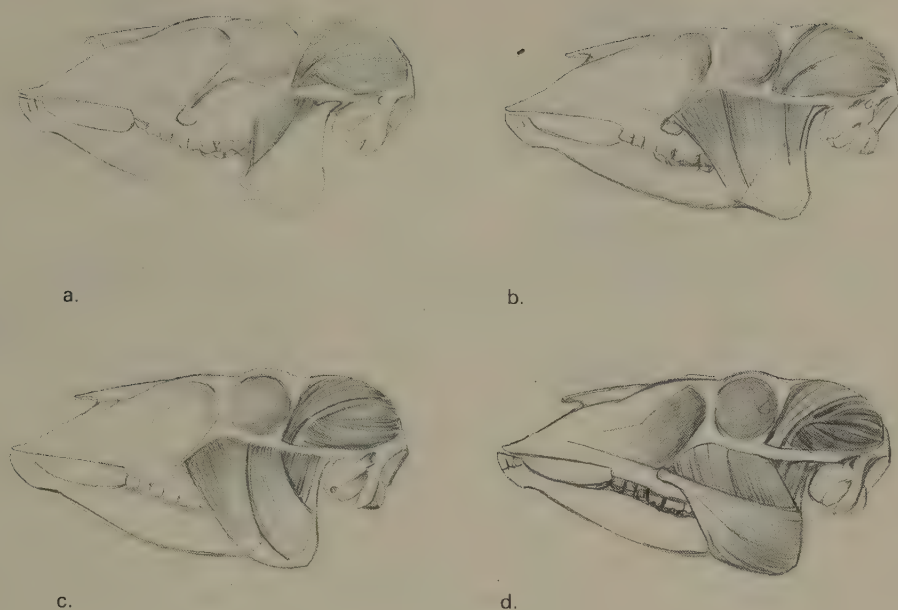
For an appreciation of how the bovid head can be transformed by a few significant alterations in the skull, the oribi, *Ourebia*, the mountain reedbuck, *Redunca fulvorufula*, and a very aberrant relative, the Cape rhebuck, *Pelea capreolus*, can provide useful illustrations. For a phyletic point of reference, the outline of a generalized skull with features appropriate to a folivorous neotragine ancestor (see p. 24) can be compared with similar outlines of the three species, their masseters sketched in as easily appreciated indicators of their dietary status.



Transformation of the head in three related antelopes: a. *Ourebia*; b. *Pelea*; and d. *Redunca fulvorufula* compared with a reconstruction of their common ancestor, c. (Masseters sketched in as indicators of fibre in diet.)

Lengthening of the muzzle in *Pelea* is probably part of an overall enlargement and elongation of the body and limbs that is related to vulnerable living in open grassland. Its diet is probably less fibrous than that of oribi and reedbuck; the teeth are narrower and the masticatory muscles less developed. The very long spike horns emerge at right angles to the top of the head (see p. 160) and extreme down-turning of the basi-cranial axis is likely to be linked with radial movement of the horn core and with allometric elongation of the face and mandible.

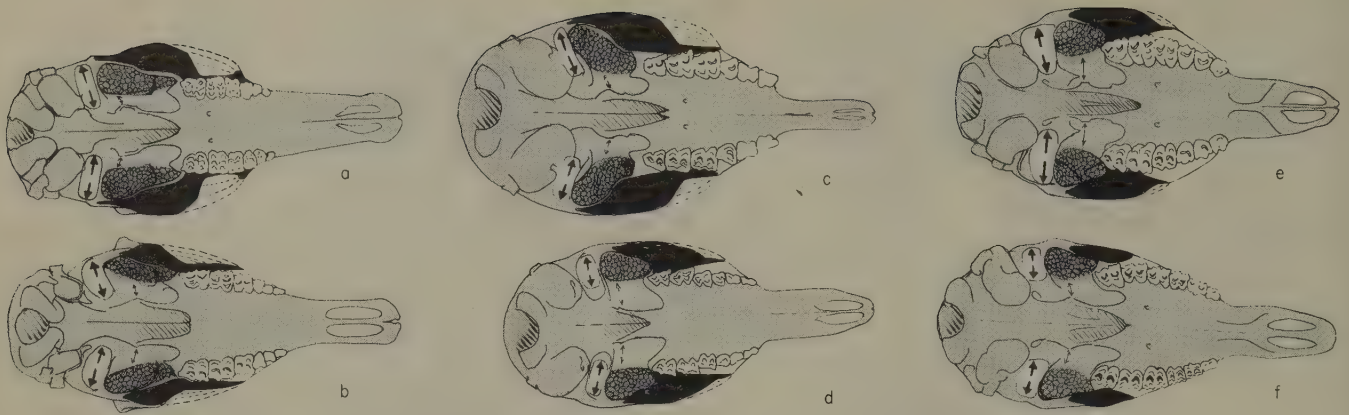
The elongated face of the oribi is also turned downwards (see p. 175) but not to the same degree. The long, nearly straight horns emerge from the orbits at an angle that is about average for a neotragine but the feature that most distinguishes oribi is grotesque development of the preorbital glands. This causes an extreme narrowing of the nasal chamber to accommodate the inflated organs that lie on either side (see p. 175). Egress of the gland over lachrymal and maxilla has shortened the masseter's reach in its superficial horizontal part. Narrowness in the muzzle must further reduce efficiency of this muscle component and oribi have compensated by greatly increasing the prominence of the bony knob on which all anterior fibres of the superficial masseter converge, (see illustration of masticatory muscles p. 25). This knob is also well-developed in the narrow-muzzled *R. fulvorufula*, as indeed it is in most reduncines.



Component parts of the bovid masticatory musculature: a. shows temporalis and zygomatico-mandibularis, deep vertical muscles; b. shows maxillo-mandibularis (lamina prima) and masseter profundus, deep relatively oblique muscles; c. shows masseter intermedius and maxillo-mandibularis (lamina secunda); d. shows the horizontal masseter.

Modest preorbital glands are a likely attribute of the common ancestor of these three antelopes but they would have been suppressed at an early stage in the branch which led to *Pelea* for this species shows not the slightest trace of their former presence.

By contrast some fossil and living reduncines show vestiges of these glands; unlikely to have reached oribi proportions, the glands of early reduncines have nonetheless left their legacy in a restricted spread of the masseter on the muzzle. However, in concert with more hypsodont teeth and deeper jaws, this muscle is altogether thicker and extends its purchase further in *Redunca fulvorufula* than in *Ourebia*. The ridge delimiting the muscle's anterior edge may be partly due to such bulking out, but this sharp margin also coincides with the boundary between masseter and the former lachrymal pit. (Also the peculiarly slender proportions of the mountain reedbuck's muzzle argue for a close relationship with the oribi.) With the area of attachment forward of the eye being limited, the deeper, vertical parts of the masseter are accommodated immediately under the orbit. This bulk of muscle, needed for a coarse diet, has required that the area of attachment enlarge substantially and this in turn makes the lower margin of the orbit jut out. The need for a widened bony base for enlarged horn cores above the orbit has meant that the capsule enclosing the eye has had to become exceptionally prominent. (The horns of the three species are discussed further on p. 162).



Ventral views of the skull in three contrasting pairs of related antelopes showing the influence of diet on skull form: a. *Redunca fulvorufula*; b. *Pelea capreolus*; c. *Madoqua kirkii*; d. *Neotragus batesi*; e. *Cephalophus dorsalis*; f. *Cephalophus nigrifrons*. Coarser diets: upper row; softer diets: lower row.

A ventral view of suborbital muscle attachments in mountain reedbuck and rhebuck serves to emphasize further that dietary habits and associated differences in teeth and musculature are responsible for the modelling of this area of the skull. The comparison can be augmented by two more examples. Because they belong to the same group and have almost identical dimensions, the dik-dik, *Madoqua guentheri*, offers a significant contrast to *Neotragus batesi*. As an exclusive feeder on soft forest floor foliage, the narrow-toothed, narrow-skulled pigmy antelope has a less demanding and less versatile diet than the dik-dik which has a robust and extended tooththrow. The influence of this on the suborbital attachment of the masseter is analogous to the situation described in the reedbuck/rhebuck contrast. An even more striking parallel occurs in the next example drawn from two duiker species with similar overall skull dimensions.

Cephalophus dorsalis has already exemplified differentiation in the masticatory function of molar and premolar teeth. In this tough food specialist direct observation and anatomical conformation confirm that the mandible makes a wider lateral traverse across the exceptionally broad molars than it does in the more herbivorous *C. nigrifrons*. Furthermore, use of the strong, pointed premolars as "champing" teeth requires a powerful vertical bite and this must add to the bulk of the masseter and extend the demand for an adequate bony anchorage. The long, narrow head and sharp, well-developed incisors of *C. nigrifrons* reflect its more herbivorous diet and its morphology is closer to the norm in duikers.

C. dorsalis has both specialized its teeth and greatly shortened its muzzle, which effectively widens its gape. Diminutive incisors oppose narrow, sharply pointed ossa incisiva or premaxilla. Whereas the mountain reedbuck has balanced protrusion of the lower margins of the eye socket with horn and orbit expansion above the eye, the bay duiker, instead, has cranial horns and the upper braincase maintains the narrow conformation of a conventional duiker. As is discussed elsewhere (p. 316), inflation below the orbits has had the incidental effect of enhancing bifocal vision in this large-eyed nocturnal species.

Protruding eye sockets in the klipspringer, *Oreotragus*, might have a similar explanation. While the eyes are exceptionally widely spaced in this species and bifocal capabilities would have an obvious utility for a rock-jumper, the klipspringer's eyes seem to protrude from the socket no more than do those of dik-diks. As in the oribi and dik-dik, gross inflation of the preorbital glands in this species has also filled out the space in front of the eyes, potentially obstructing vision and prohibiting the masseter's extension in front of the eyes which further concentrates this muscle's attachment below the orbit. Because of their orbital base the upright horns have also migrated apart and are exceptionally widely spaced in the klipspringer.

Considering that horns are a major external characteristic of bovids, it is odd how little attention they have received. Geist (1966a; 1974b), Schaffer and Reed (1972) and others have begun to rectify this neglect but the central importance of horns in the evolution and biology of bovids and the potentials for ecological and social correlations are not generally appreciated. It has already been pointed out that horn types provide one of the criteria for dividing the bovids into two major divisions. The sub-family Bovinae can in turn be subdivided on the basis of horn shape. Some tribes of Antilopinae have solid, others hollow frontals and horn bases (p. 14), a further tribe, the duikers, can be diagnosed on where and how its horns are rooted (p. 264), and another, the reduncines, on the ontogeny of horn development (p. 164).

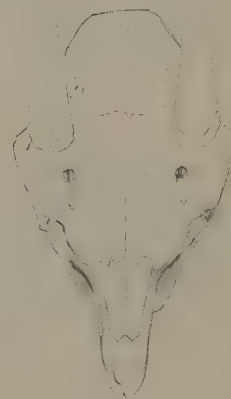
What are the origins of horns? Numerous fossils testify that the early pecoran ruminants went through a prolonged phase of experiment during which all manner of ossified lumps and bumps and spikes appeared on the upper surfaces of the skull. One of these experiments gave rise to the cervids, another to the bovids.

For the cervids a good fossil record can be augmented by evidence from living species to show that antlers arose as defensive devices against wounding by canine tusks. Goss (1972) has implied that there may be a meaningful relationship in the resemblance of some wound-healing processes to the process of antler regeneration. Barrette (1977) has documented the use of antlers in the tusked male muntjac, *Muntiacus*, to neutralize the tusk slashes of another male during fights, as well as their secondary use for body strikes, head-on clashes or for leverage to throw an opponent.

No such evidence exists for early bovid horns (which are physiologically a fundamentally different structure (Modell, 1969). Indeed, the bovids probably emerged as a recognizable group only after horns had ceased to have a purely defensive function and were already well-developed weapons of offence.

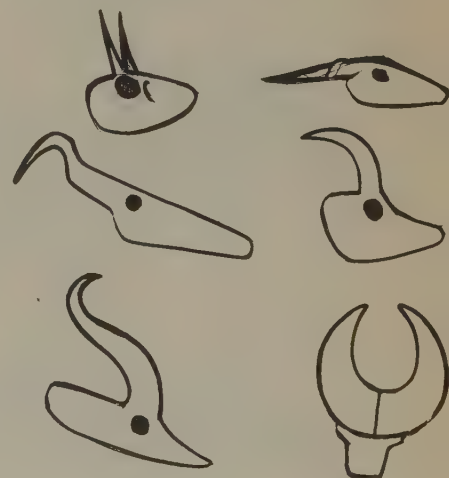
Although bovid horns are also likely to owe their earliest origins to tusk fighting, the only sign of that phase of evolution is an occasional propensity in some antelopes to bite (see pp. 198, 576).

The most primitive types of bovid horns were probably pronged structures or one or more pairs of sharp, short spikes. A single pair of spikes is ill adapted to use in head-to-head combat and it can be related in living species with an agile, whirl-around stabbing contest which culminates in a fast chase, wounding, or the death of one or both contestants. Although the more superficial features of such a contest do not differ greatly from those of chevrotains,



Top view of klipspringer skull.

A bovid's head is transformed by the shape and orientation of its horns.



several major changes in anatomical structures, fighting methods and defensive orientation are implied in the switch from a slash inflicted by the downward stroke of bladed tusks to an upwards stab from pointed horns. Perhaps the most important structural change was emancipation of the mouth so that it could be wholly devoted to food gathering. The most significant differences between primitive horns and primitive antlers was that, while the latter tended merely to neutralize or supplement use of the canines, bovid horns (or their precursors) not only proved to be a deterrent but an effective alternative rendering tusks obsolete at a very early stage. Nonetheless, unelaborated spikes are crude weapons with very limited uses. How these rather unsatisfactory weapons and modes of combat have been elaborated is discussed in subsequent profiles, but it must be stressed that much remains to be learnt. Before we can fully understand the evolution of horns, the details of fighting technique and ontogenetic growth need to be studied in all major species.

The major functional zones in the horns of advanced social types are discussed in the profiles of individual species and tribes, particularly for the Antilopinae. Simple horny cores have been drawn out into a multiplicity of shapes and, in the most fully developed types, distinct catching, ramming, hooking and stabbing zones can be identified; in the less social species only a few of these functions are operative. Only tragelaphines seem to have a simple relationship between horn size and body size.



Functional zones in a multi-purpose antelope horn (from tip to base) spike, catching arc, ramming arc and stem.

The physiological basis for elaborating the shape of a horn seems to be contained in the mode whereby material is laid down in the horn sheath. Horn contains innumerable fine tubules that are the empty centres of dead cells and the horn fibre consists of these dead cells welded together by keratin (Gadow, 1902; Trautman and Fiebiger, 1952). In a very young bovid the epidermis at the horn site consists of four layers, the outer *stratum corneum* being composed of horn tubules and fibres which overlie a layer of granular cells, the *stratum granulosum* beneath which lie the *stratum spinosum* and *stratum germinativum*. It is to this inner layer, which covers the horn core, that the filaments of the horn owe their origin.

The keratohyalin granules in the *stratum granulosum* are an intermediate stage in a transformation whereby cells that still contain cytoplasm and nuclei when in the *stratum spinosum* degenerate as they become completely keratinized in the *stratum corneum*. In the opinion of George (1956), the horn tubules, which once constituted the *stratum granulosum*, appear to contain a homogeneous substance which sticks the horn fibres together to make the compound material we call horn.

right: waterbuck
(reduncine)

left: sable
(hippotragine)

right: kob
(reduncine)

left: oryx
(hippotragine)

right: impala
(alcelaphine)

left: damalisc
(alcelaphine)

right: Thomson's
gazelle
(antilopine)

left: hartebeest
(alcelaphine)

right: Grant's
gazelle
(antilopine)

left: gnu
(alcelaphine)

right: gerenuk
(antilopine)

left: buffalo
(bovine)

right: goat
(caprine)

left: sheep
(caprine)

The early stages of horn growth are characterized by this step-by-step degeneration of cells which produces the impermanent, flaky, soft keratin of the juvenile horn. Hard permanent horn is formed by a more abrupt keratinization of cells in the *stratum spinosum* (George, 1956). It would seem that rates of growth and deposition around the growing cone and later the base of the horn can vary around its circumference and can alter with time. Growth patterns clearly differ from species to species (and in some species from one population to another).

A straight symmetrical horn shows a very even rate of deposition around the horn core. When the horn is arched in a single plane, as it is in some reedbuck and in the sable antelope, the quantity of material laid down on the outer curve is consistently thicker and covers a larger area of the core than on the inner curve. The bony core, which would probably be straight without this influence from its horny sleeve, follows the arc imposed by this uneven growth pattern (see p. 162). Noting that keratinous horns can sometimes develop without any bony core, Duerst (1926) considered that horn form, notably the basic cone shape, is determined by the sheath not the core. D'Arcy Thompson (1942) (who took a mechanical rather than an evolutionary view of horns) also ascribed their curvature to differing growth rates on opposite sides of the sheath base (see p. 591).

Thicker areas are not always the faster growing. Tragelaphine spirals derive from a faster rate of growth in the thin, main sheath against a slower rate in one or two localized points within the circumference of the horn. In the "bladed" species; sitatunga, bongo, bushbuck, one of these slow-growing points is the sharp edge of the horn core behind the orbit, the other the dense ridge arising from the forehead. In the kudu-eland group, the faster-growing shaft slews around the pivot of a single heavy ridge (see p. 75).

Where the horn forms an eccentric shape, as in the lyrate horns of impala or kob, or the bizarre twisted hooks of the hartebeest, the differential deposition of horny material has more than one temporal rhythm. There is the growth "pulse" that produces corrugations or annuli on the surface. This is superimposed upon staged periods of uneven growth that produce arcs or twists in a predetermined direction, followed by other periods when the direction of growth may alter or be reversed. Fossil evidence suggests that such complex patterns of growth and their implied genetic clocks have been determined by the species' evolutionary history. In such species it is possible that the core is not the malleable stem it seems to be in species with a simpler growth pattern (see p. 442).

Well-developed horns require substantial bony anchorage in the skull. Even more important, their leverage requires that the skull, vertebrae and neck muscles must have mechanical properties appropriate to the size, conformation and function of the horns. Some attention has been given to this aspect of form and function in the profiles of reduncines, gerenuk and alcelaphines. Devices for increasing leverage or absorbing the stresses of greater impacts from blows have far-reaching effects on the architecture of horns and general morphology of antelopes but much remains to be learnt.

Apart from their use as physical weapons, horns are even more frequently symbolic weapons. Tilts or jabs are obvious threats but there is abundant



Axis of a kudu horn (after Zehntner).



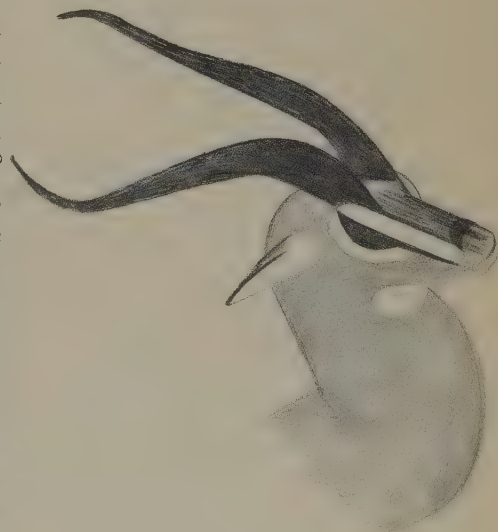
Geometry of frontal and profile views in oryx, sable and waterbuck.

evidence that antelopes convey their status or future intentions by very much less conspicuous movements, perhaps the size and shape of horns alone provide information to conspecifics. This is particularly true for all the Bovinae and for those Antilopinae that have social hierarchies where such economic signals may play a part in maintaining the social status quo.

A ferocious attack or complete indifference may be elicited in a male antelope by small differences in the carriage of another male's head. What appears to be a normal grazing posture, a quick lick of the lips, or a flick of the ears or tail can actually signal status and predict future actions. It is well-known that a bull shows the whites of his eyes in a challenge, but we need to know much more about the role of eye movements and the signal value of a "look". Eyes are totally disguised in the Antilopini and Hippotragini by bold facial stripes which often continue the line of the horns down the sides of the head. Eyes are hooded by thick coat-coloured lashes in *Alcelaphus*, yet they are advertised in reduncines by pale surrounds—why? There is probably some sort of structural relationship between eye signals and social organization in these different tribes, but such subtleties have yet to be studied.

By adjusting the angles of three units, head and horns, neck and ears, bongo, roan antelope, topi and other members of their tribes can produce striking visual conformations, and it is likely that some superficial face and ear markings have evolved as an integral part of this iconography. For example, the bridge of the nose is marked by white flashes in most tragelaphine species. In most postures it is one of a small constellation of light markings that can form remarkable geometries when the animal presents a symmetrical view, as when the head is erect and looking straight forward.

Horn tilting in Grant's gazelle.





Sitatunga, *Tragelaphus spekei*.

In such a position the muzzle markings form a straight bar across the face, but should the animal lower its head they become a "V" which exactly matches that of the horns converging on the forehead above. Such a view is only presented by a female incidentally to its feeding. Males advancing in this position are generally making an unambiguous threat. The shape may therefore act as the symbol of such a threat while it simultaneously helps to demarcate the boundaries of action for those animals that take on the challenge. This could be important when the horns are not in themselves conspicuous, and demarcation of the weapons' boundaries and size may also explain the pale-coloured horn tips in bongo, sitatunga and bushbuck.

"Flagging" of the head and horns is particularly conspicuous in long-horned species such as the kudu and Grant's gazelle, where it is part of species-specific behaviour during confrontations. In these and many other species such ritualized displays and vigorous horning of the ground or vege-

tation may be the prelude to a clash or fight, particularly in the younger males. There are, however, differences in the role of horns in antelopes with dominance hierarchies and territorial species. For example, it is common for all horned bovids to attack inanimate objects when excited; in a rank system such a display signifies an individual's potential as an aggressor and the attention of other herd members is on the animal, with the horns a momentary focal point while it savages its surroundings. In territorial species, the same action is more significant for the *place* in which it is performed; the horns' onslaught on earth, bark or twigs augments a barrage of labels which associate the *area* with a potential for aggression. Such a shift from direct to indirect use of weapons may lie behind the evolution of corrugated, abrasive surfaces in the horns of territorial bovids. (Hierarchical organization is almost certainly a secondary development in those species that combine this social order with annulated horns.)

Horning of the environment rather than a rival is energy-saving for antelopes of either sort but only serves a function if it elicits appropriate behaviour in conspecifics. When the relationship between males is untested or needs frequent re-testing, as in age classes that are still growing, or when an unknown intruder appears, the outcome of a confrontation is usually a vigorous fight. Already established relationships do not need such energetic tests and status can be reinforced by various forms of indirect horning, including "flagging" displays. In territorial species confrontations between neighbours tend to become protracted routines which can be actively sought by one or both animals, often at the same place and time of day.

Typically each animal approaches with an ostentatious gait, displays its head and horns with very contrived movements and artificially bulged neck; it marks with glandular secretions, dung deposits and scrapes with horns and hooves. Horning the earth, flagging of the head and cushion fighting may all be components in a string of stereotyped actions that take place along an established frontier and serve as a ritualized beating of the bounds. Sparring and circling, if they take place at all, are desultory and are followed by a return deeper into the territory or a procession along the boundary. A common aftermath of the ritual is more gland marking activity, a trait that occurs in almost all territorial antelopes. This activity can be seen as a very important energy-saving device. It greatly reduces chases and counterchases, because the presence or absence of ownership signals strongly prejudices the outcome of a challenge and aggression visibly wanes in many species the further they get from their scented homeland.

Some elements of antelope displays might originate in the way day-to-day meetings between conspecifics are managed or avoided and chance encounters need signals which are basic to a species' repertoire. When tragelaphines, neotragines, duikers and reedbuck first come across conspecifics in dense cover they often emit one or more cries as they make a short preliminary run momentarily flashing tail or rump. Many such occasions are probably accompanied by massive emissions of scent from glands on legs, groin or head, but humans watching such behaviour are perforce like spectators of a silent film and one can but guess at the type and intensity of olfactory message that is being broadcast.

Sound and, for many species scent, serves to localize the presence, move-



Grant's gazelle displaying.



ment, direction of flight, sex and often the identity of an individual. Messages can alarm, deflect, warn, appease, challenge or serve as adjuncts to sex or territorialism, depending on the caller, recipient, site and context. The nature of cries and their ontogeny in some of the neotragines suggest that they may originate in the quick breaths of a small animal trying to pick up scent from a disturbance. The grysbok stamps its scent-glanded hoof as it makes its call (p. 206). A dik-dik sometimes flares white rump fur as it bounces away with wheezing cries (p. 259). Inguinal glands are the cause of a popping noise when reedbuck leap away, whistling and bobbing their white tails and rumps (p. 338). Impala generally flee in silence as they make high kicking leaps which probably scent the air from their large fetlock glands (p. 464).

While sound and scent signals probably allow well-established neighbours to identify individuals, information content in the momentary view of a white scut or fleeing rump is very restricted. Apart from the obvious "I'm leaving", a rump view frequently offers the supplementary message of "I'm inferior". At close quarters visual indications of sex are insignificant because olfaction offers a more effective channel of information.

Apart from some strongly structured patterns that are probably designed to operate at very close quarters (see p. 72), the visual signals of antelopes from dense habitats tend to be of less developed types.

The scope for visual communication increases enormously when visibility in the habitat improves but scent and sound remain the major communication channels for most antelopes, because greater conspicuousness tends to invite higher mortality from predation. It is therefore significant that coat patterns and associated signalling behaviours are most highly developed in mobile classes (not in the infants) of fast open country species, such as gazelles, some alcelaphines and oryx (the bongo and some other tragelaphines are special cases), p. 168.

In such species the rump remains a focus of sexual interest and of appeasement and "departure" signals. Because mechanisms for damping or deflecting aggression are important for the regulation of most types of social order, there is likely to be a direct relationship between the enormous variety and range of rump signals (Guthrie, 1971) and the counteraction of aggression. For the patterns to serve such functions they need to be presented with particular postures and in appropriate contexts, sometimes accompanied by special calls or emissions of scent. The absence or suppression of such patterns, as in the klipspringer, may imply a shift in the focus of signals to other parts of the body or to other modes of communication than the visual.

The "intention movements" of foot stampings, whether augmented by glandular emissions or not are advertised by black and white flashes in many species. High stepping may be emphasized by knee or upper-leg patterns and these may link with contrasting bands on the flanks. The latter tend to correlate with "broadside presentation", a manipulation of the body's orientation that tends to advertise specific qualities to conspecifics but can have very varied connotations (p. 101).

The ritualized encounters between male rivals that were described earlier also employ visual patterns to emphasize particular qualities of a specific



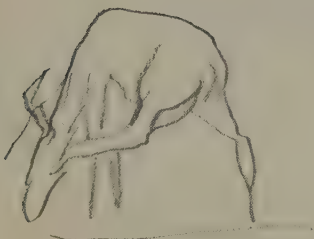
Above: impala.

Below: dik-dik.





♂ Flehmen, excited by goshawk



display. Rival tragelaphine males go through a protracted ceremony in which the animals slowly circle with bulging necks, raised crests, high steps, flicking heads and finally horn clashing, but there are other species where very similar actions and sequences are conducted at the gallop, notably the gnu (p. 533) and the oryx (p. 580).

Such eye-catching cavortings are often lumped under the terms "pronking" or "stotting". These names have been used to describe a variety of bouncy gaits in which the body assumes contrived positions which usually represent particular gestures "set to motion".

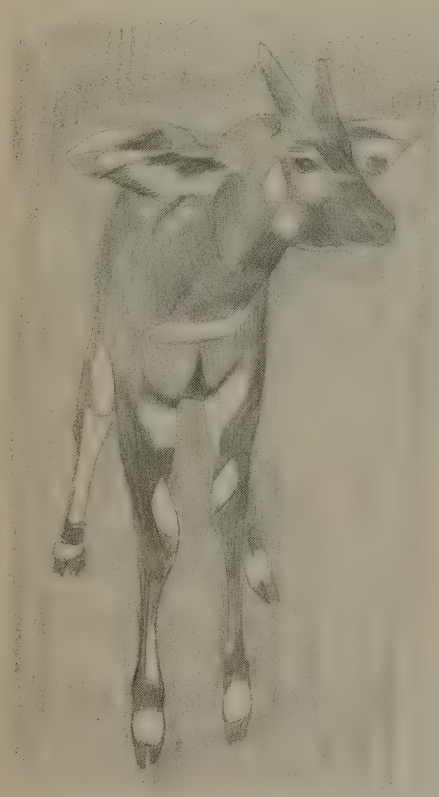
"Pronking" is not restricted to bovids; similar movements appear in the insectivore *Rhynchocyon* and in the long-legged rodent *Dolichotis*. Dubost *et al.* (1974) has described this as a form of play in juvenile *Dolichotis* and a sign of moderate excitement. Likewise, pronking and related gaits are commonly seen in juvenile antelopes and most frequently when they have been excited by a change or the appearance of something new or strange in the surroundings. It may be associated with changing light, temperature or wind (particularly in the early morning); a universal characteristic of the stimulus is the arrival of something that threatens the individual's contact or orientation with respect to particular conspecifics or a particular locality. Thus a young male hartebeest first assumes a very vertical appeasement posture when a territorial male approaches. Because the mother is both the object of interest for the latter and the centre of existence for the former, the young animal is unable to flee very far even if threatened or chased. It therefore circles the mother, quacking like a goose and bouncing along with high floating bounds in which the vertical appeasement posture is artificially maintained (Gosling, 1974a).

The potential of such displays is very varied and Kruuk (1972) has suggested that gazelles mediate the activity of conspecifics by conspicuous pronking, and he has pointed out the utility of such a co-ordinating function after groups have been disrupted by a predator. Similar behaviour may help to co-ordinate and re-orient members of a group during more routine movements, as sometimes appears to be the case in impala, where a major function of ritualized leaping seems to be maintenance of group cohesion (p. 465).

The optical, auditory or olfactory stimuli broadcast by a pronking or bouncing display may be so emphatic that they effectively "force" a reaction from neighbours; certainly pronking commonly precipitates or invites imitation, hence the common observation that the activity is "infectious".

Imitation is an important and little-studied aspect of bovid development and learning. It has been observed that isolated juveniles reared with other species of antelopes often attempt to imitate their greeting or challenge gestures and particularly their ritualized gaits. For example a young damalisc has been seen to copy a gazelle companion's stotting and join a reedbuck in clumsy side-to-side jinking (Bonarius personal communication). Neither of the gaits normally appear in damalisc herds.

The potential for coercing other group members invests the pronking phenomenon with a social utility that may go beyond simply warning, appeasing or keeping together. A more complex web of these and other components may be present in the oryx "tournament" (p. 580), which appears



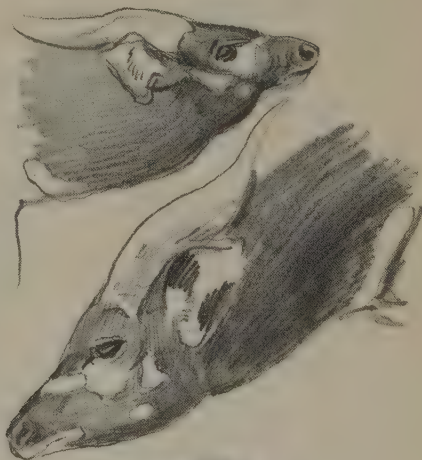
to reconcile such disparate elements as challenge to one class and reassurance to another. In a hierarchical society the tournament may allow young animals to establish their own order and to test and develop their physical strength within a herd of dangerous adults without setting off an attack. Carried over into adult life such a function could be extended in that vigorous activity by adults, so long as it is identifiably ritualized, need not cause other group members to scatter or attack. Thus reassurance and challenge can be integrated in a single, complex display sequence in which a succession of ritualized movements and peculiar pacing gait combine with coat colour to produce a spectacular species-specific performance.

In the text that follows, less dramatic attitudes will be analysed for their communication content, and the visual bias that has run through other volumes will be evident. It is a bias that cannot be avoided in a book that is in large part an exercise in looking at animal form. I remarked in Volume I that external appearances have often evolved and been selected for in direct response to the faculty of visual perception in other animals. There is abundant evidence that appearances influence behaviour (particularly in conspecifics) in innumerable situations. Hediger (1949) coined the term "static-optic marking" to describe the self-advertisement that is so typical of solitary antelopes standing on the open plains. His use of the term "marking" stressed the existence of an iconography but the implicit simile with scent-marking serves to underline our ignorance of mammalian communication, whether the medium is olfactory, visual or auditory.

Understanding the "marks" that have been evolved by animals as visual signals may eventually open up areas of investigation where lines between art and science are narrowed. Apart from our own untapped resources for visual communication we have scarcely begun to develop awareness of this aspect of form and function in the biological world.

For example, the visual effects and illusions of stripes and other repeat patterns are evident in various tragelaphine antelopes as well as in zebras, striped mongooses and hyaenas that were discussed in earlier volumes. Such visual devices have been explored by artists in various ways for centuries, culminating in the "Op(tic) Art" school of painting. Following the development of micro-electrodes it has become possible for neuro-physiologists to explore some of the effects of stripe patterns on perception in mammals. A most important finding has been that individual nerve cells will only respond to particular visual stimuli, such as edges with a definite and constant orientation or a pattern presented at a specific distance. A cell may be tuned to a single colour in species that can perceive it. Experiments have shown that some nerve cells respond to particular spatial frequencies (Blake-more, 1971; Mollon, 1974) and Mollon remarked that human responses to visual after-effects that have been induced by experiments with striped repeat patterns are in some ways akin to the phenomenon of conditioning. This may have considerable implications for mammals, as the strong visual effect of striping and other bold signal patterns could be employed to reinforce and direct various species-specific behaviours. The possible function of stripes in the biology of the bongo is discussed on p. 72. Other signal codes are discussed for lesser kudu (p. 111), dik-dik (p. 255), gazelles (p. 415) and Alcelaphini (p. 450).

Above and opposite:
bongo, *Boocercus*.



Lesser kudu,
Tragelaphus imberbis.



Our mental image of a species is often very dependent on some superficial peculiarity of pattern and in this respect the drawings of flayed animals are an important part of this study. They are not meant to conjure up visions of a butcher's shop, nor the neutral labelling of an anatomical treatise, rather they are intended to display those still living animals that hide, not beneath bushes or rocks, but behind a facade of manes, dewlaps, tufts and gaudy markings. They are intended to ease comparison of proportions and allow physically functional form to be appreciated. Perhaps even more important, they indirectly promote a recognition that pattern and colouring *communicate* and that they constitute a distinct and self-contained system.



Such a presentation allows a superficial pattern to be explored as a separate element. The classic behaviour studies by Tinbergen and Lorenz revealed that animals transmitting visual signals limit them to a significant part of their bodies while recipients are sensitive only to that part or to crude models of the signal. I have shown for guenons (Kingdon, 1980) how similar optical signals can be employed towards different ends in closely related species. While a superficial but strongly geometric pattern can incidentally serve to reduce ambiguity; it can at the same time elicit an instantaneous and highly species-specific response. Some of these geometries cannot fail to catch the eye, even of a slow human observer, and they often come into prominence if one attempts to sketch, as the drawings on p. 31 show.

The fact that optical signalling equipment is an integral part of the animal's appearance has meant a disproportionate attention to visual communication in this work and dependence on pencil and paper as tools has reinforced this bias. The investigation of visual modes of communication continues to depend upon patient observation with minimal reliance on technology, whereas new techniques for molecular and chemical analysis of pheromones and electronic recording of vocalizations have opened up new possibilities for the investigation of olfactory and auditory-based systems.



Trying to make sense of optical signals is but the symptom of a much broader and widely-shared effort. Interpreting the innumerable patterns that emerge from their observation is a preoccupation of most naturalists and biologists and there has been much stimulating enquiry, particularly in the last decade.

With functional relationship between ecology, morphology and social organization being shown for birds (Crook, 1965; Verner and Willson, 1966), primates (Rowell, 1966a; Gartlan, 1968; Crook, 1970a) and insects (Wilson, 1971), the bovids were soon examined from similar perspectives. Various aspects of the behavioural ecology and anatomy of bovids and other large herbivores have been explored by Estes (1974), Geist (1971b, 1974a, b), Gosling (1974a, b), Hofmann (1973), Jarman (1974) and Leuthold (1974, 1977b).

Common to all these studies has been the attempt to place particular elements of the animals' biology within a broad ecological framework. Geist (1974a) has provided the most thoughtful theoretical base for relating ecology to social evolution and he has isolated some basic principles and twelve significant ecological parameters. He has also correlated the morphology of bovids with broader aspects of their biology. Estes (1974) has followed Ewer (1968) in regarding terrain and type of food as the two factors which most influence social relations. Drawing from first-hand knowledge of the behaviour and ecology of several African species, he correlated the socialization of bovid species with a transition from closed to open habitats, an interpretation that has been touched on in earlier pages and for the Tragelaphini is probably correct but, with respect to the Antilopinae, is the reverse of the scheme followed in this volume. Gosling (1974a) made a model dissection of the structural links between ecology, behaviour and morphology through the painstaking analytical study of a single species, the hartebeest, and other monographs of species have also integrated these elements with success. Hofmann's seminal and wide-ranging study of stomach morphology (1973) used feeding habits to define a number of dietary classes which, while documenting the foods and feeding techniques of many species of African antelopes also drew attention to other correlations, such as special behaviours to avoid predators, peculiar body architectures, small social groupings and dispersed feeding in "concentrate selectors"; a tendency towards large herds and movements after food and water in the larger "bulk and roughage" eaters.

Jarman (1974) incorporated many of Hofmann's observations on dietary types but modelled his approach on Crook and Gartlan (1966) and Crook (1970b) and he attempted a very similar codification of habitat, diet, group size and social behaviour. On the argument that a major part of social organization derives from the strategy males use to obtain maximum reproductive effectiveness, the particular nature of this strategy must depend upon the distribution of females and the size of their groups, which in turn are dependent on the temporal and spatial distribution of the species' "feeding style". Jarman used social organization as the base-line for supposed correlations with seasonality, predation and group size; a parameter that is highly mutable, often being readily altered within a single species by differing population densities. As a result several of his alphabetical classes

were erected on sand. Leuthold (1977b), like the preceding authors, emphasized diet as the ultimate determinant of population dispersion and social structure. Although he pointed out the considerable difficulties of assigning real species to theoretical classes, he succumbed, nevertheless, to the tidy conceptual attractiveness of Jarman's classification, in common with other reviewers.

As a result of these studies we are closer to understanding the structural relationships between very different aspects of bovid biology but the opacity of relationships between many living species and groups has led to a tacit avoidance of bovid phylogeny, an area in which the palaeontologists Gentry (1970a, 1978a, c) and Thomas (1979a, b) have been the outstanding workers in recent years.

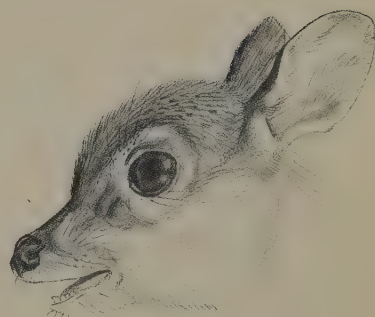
From Schlosser (1903) to Leuthold (1977b) every attempt at classification has tended to group a different permutation of bovid species according to the parameters chosen as baselines. Dentition, physiology, stomach structures, feeding style, social organization or body size each produce different combinations. This reflects the fact that the bovid radiation has produced lineages that often parallel one another in some respects (notably adaptation to more fibre in the diet and increased size) while conforming to strict lineage rules in others.

A recurrent topic in bovid biology has been the apposition of rules that are determined by size, diet, physiology etc. with supposed phylogenetic determinants. It is not always remembered that ecology and phylogeny are not wholly separable entities; it is not ecology but natural selection that has determined which, in the long cavalcade of extinct and extant species, should be the ones that are present and best able to respond to various situations as they arise.

For example, it is obvious that greater kudu and the smaller tragelaphines cope with predation in a quite different way to bongo and eland. The first two have a scattered, essentially independent if not solitary existence and both females and young rely on crypsis to evade predation in their dense habitats. Bongo and eland represent the largest forms of two separate tragelaphine lineages; because of their size each has had to adapt to travelling further for their food and this, together with their size, has rendered crypsis ineffective. In both species the females form larger, tightly knit groups while they are accompanied by vulnerable young and in both species this can occur during seasons when their nutritional needs would be better met with the normal tragelaphine scatter. On the face of it the formation of herds seems to be a direct response to high levels of predation, but the animals' morphology betrays the existence of a built-in alternative strategy—*counter-acting* rather than evading predation (a major limiting factor on any tragelaphine species).

The independent development of horns in the females of each lineage represents their common evolutionary response to the challenge of predators. The utility of horns lies not only in their use against predators; once a group has been formed they become the instruments of a social hierarchy (and may also serve as useful tools to break branches).

Female horns are therefore a structural correlate of the socialization of these species and predation can be identified as the selective pressure



Above: mouth of leaf-picking suni.

Opposite: mouth of roughage-grazer, the buffalo.

inducing the formation of herds at phylogenetic as well as phenotypic levels.

By its attachment to dense cover the bongo demonstrates that it is not necessary to abandon concealment to become social and an examination of other species suggests that predation is by no means a universal factor in the socialization of bovids.

Other environmental forces, floods (see p. 332) and the universal attraction of food frequently force animals into dense aggregations. Such disparate forces produce different types of aggregation and there is no close correlation between high density and a strongly structured social system. Sitatunga and bushbuck sometimes achieve local densities that compare well with those of kob or impala yet they develop little more than rudimentary hierarchies. In this as in many other aspects of their biology the Bovinae and Antilopinae are very different.

Wherever aggregations are seasonal their character is greatly influenced by timing in relation to the reproductive cycle of a species. The topi provides a particularly well-documented example of how varied and versatile a species can be in adapting its social responses to different densities and variable sequences of events (Jewell, 1972; Duncan, 1975; Monfort-Braham, 1973).

Topi, gnu and kob are species in which conventional spaced-out antilopine territories lose their utility as female numbers, density and mobility increase. Clusters of strategically placed males are therefore better able to serve the needs of females in mega-herds, and the varied responses of these species are described on p. 490.

In such situations elaborate communication systems break down and only very exaggerated olfactory, auditory or visual signals are effective. Thus high-density breeding populations of topi, gnu, kob or impala can be noisy, dramatic and sometimes smelly. The contrast between an individual antelope's behaviour at low and high densities can be anthropomorphized as that of a man tilling his home field and one competing in a bazaar.

Territorial and dominance behaviour in bovid males is a product of the reproductive process, but because the main incentive for a female's presence in a particular place is always food, competition is often indirect and males fight for territories not females. If resources are evenly scattered and reliable and the animals spaced out in singles there is no significant selection for greater size or any other form of sexual dimorphism except in one particular: in many solitary or pair-forming territorial species the female is hornless. Hornlessness seems to be equivalent to a sort of physiological extension of the juvenile condition (many female neotragines have distinct horn buds above their orbits). Because the absence of adult characteristics is a potent inhibitor of male intolerance, females can gain access to prime pastures without being molested by males. This leaves the female free to eat and breed (subject perhaps to being herded when near a boundary). The function of regulating access to the home range becomes a male specialization in all such dimorphic species, but wherever females are horned they take on an active part in regulating their own share of such resources (see p. 491). The development or suppression of horns in female antelopes is therefore not a fixed trait, it is neither primitive nor advanced, rather it is the symptom of a mechanism for gaining access to resources, whether by weaponry or by the artifice of defencelessness.



When food resources are abundant but uneven in time and space, groups of females may still benefit from being hornless as they travel through territories from pasture to pasture, but they derive an extra benefit from a territorial male's wardship when they are in oestrus because the cumulative effect of unbridled male competition is one prolonged exhausting chase.

For horned females quiet havens are less of a consideration than the quality of food in a male territory. In such situations males with places in the best habitats greatly increase their share of matings but they have to fight long and hard for their land. For example, *Alcelaphus buselaphus* have evolved complex heavy horns which can probably be correlated with frequent and intense fighting.

In species with hierarchies there is also some correspondence between heavy horns and higher social densities (bigger herds) both within a species (i.e. forest and savanna buffaloes) and between species, such as the kudus and eland.

Greater kudu,
Tragelaphus strepsiceros.

In species with short, concentrated breeding seasons, rapid alternation between fighting and courtship is both exhausting and requires exaggerated signals to reassure females about the males' intentions. An almost universal courtship posture contrives to hide the male's horns while he approaches the female. This lowered-head chin-up gesture may derive directly from urine testing or *flehmen*, but it is frequently so highly ritualized that its most striking effect is to display prominent, chin, face, throat or ear markings. Courtship display and the reproductive behaviour of many species are described in the profiles as are the varied characteristics of births, growth and maturation. Reproductive patterns are highly variable and in some cases the determinants of breeding seasons are probably best understood by totting up disadvantages and finding the time when a species faces the fewest obstacles.

The conditions under which animals live and are studied today are often far from optimal and the animals themselves may merely contrive by various makeshifts to survive, indeed they may not be perfectly adapted to their habitat. Given our ever-increasing plunder of the land, a dogged capacity for survival must seem the only hope for the future of many species but it cannot diminish our responsibility. We cannot afford to dismantle much further the complex webs, chains and pyramids of organic life that we are privileged to see in East Africa today.

The account of antelopes that follows concludes this book. It completes the inventory of a complex mammalian fauna in a region that I have tried to demonstrate is pivotal to our understanding of evolution.

In terms of ecological impact and significance, economic potential and scientific interest antelopes are probably the single most important group in this inventory. Most of the information, whether it concerns morphology, distribution, ecology or behaviour can be rendered as measures of relative size, weight, area, activity and so on. With the accumulation of more and more data mathematical and statistical treatment becomes progressively more imperative. As that useful tool, the computer, allows us to discover much wider ranges of correlation between enormous numbers of variables, biologists and particularly ecologists are expressing themselves directly in mathematical and statistical terms to a greater and greater extent. It is highly desirable that we should learn to see the patterns in which cells, animals and larger units occupy space and time as complex, active, and highly abstract entities—here lies the way forward.

As we move on, with new techniques, into ever more complex realms of thought and endeavour there is still room for the naturalist's rather piecemeal approach that has been employed in these volumes. Every profile has begun with the physical form of an animal and this I have attempted to probe with mind and pencil without losing a direct, visualized consciousness of its living presence—hence the abundant drawings.

So long as we can still experience that presence, so long as we can still see for ourselves the particular places and spaces within which these animals live out the drama of their lives we can but be left with the knowledge that these measured compilations of abstract matter that have been organized into what we call "species" or "ecosystems" are creations of matchless beauty to which no human skill or mind can do justice.





Eland. *Taurotragus*.

Bovines

Bovinae

Tribes

Bovini

Tragelaphini

The characteristics which distinguish bovines from antilopines are larger size, an absence of facial or pedal glands and smooth or keeled rather than annulated horns. Less immediately obvious but highly significant differences are that most if not all Bovini are relatively mobile and, instead of forming exclusive territories, have hierarchies.

Antilopinae are more highly diversified but they have all derived from smaller ancestors possessing facial glands which, when combined with the size difference, implies territorial ancestry.

The characteristics listed above suggest that the primary divergence between the ancestral Bovinae and the ancestors of the smaller gland-owning eotragine/neotragine antilopine lineages had an ecological basis.

Sedentary territorial animals need a reliable food supply. If they are small they can be supported by a wide range of vegetation types and their size will determine the extent to which olfactory systems for demarcating occupancy are anatomically and physiologically feasible. Selection for the common mammalian system of scent-marked territories will be strongest where there is a tight fit between the practical defensibility of an area and its provision of food and shelter for reproducing animals. The fit is probably best in habitats where food is not super-abundant, because a balance must be achieved between population density and the overall year-long needs of mutually intolerant individuals.

If food is locally unreliable animals must make periodic movements or become nomadic and selection for territorial behaviour or its associated anatomical structures is reduced or absent. Animals can only use an unstable habitat if their off-season food is predictable and within reach and if they are adapted to the demands of an unstable existence. There is a congruence here between the bovids' reliance on the food being there, the viability of territoriality and the functional implications of body size. The environmental conditions that introduce seasonal instability in food at the same time as ensuring an off-season alternative nearby also tend to produce concentrated areas of super-abundance.

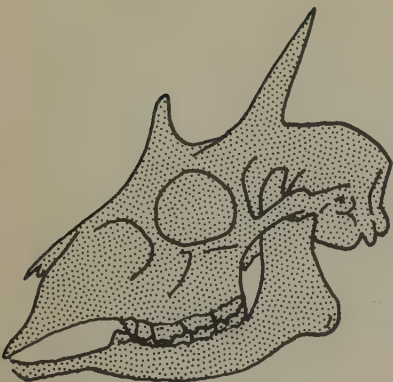
A bovid that has to move in search of food can acquire the advantages of more economic, efficient locomotion and a reduction of vulnerability to predators if it increases its body size. This must be sustained by the certainty of adequate food and this in turn may involve fluctuating densities. In such situations there is selection for a *modus vivendi* between intolerant individuals, and the practical expression of this is rank hierarchies, primarily between males.

Hierarchical relationships introduce sexual selection in favour of the larger male and it is this factor which has probably caused the Bovinae to evolve such very much larger forms than the Antilopinae; the weight differences can be appreciated on pp. 18, 19 (note that page space has demanded contraction of the graphic scale indicating bovine weight ranges). There is fossil evidence that the Bovinae, which have undisputably Asiatic origins, had a long head-start with respect to body size.

A very early adaptation to the combination of abundant but fluctuating food supplies might therefore lie behind the absence of facial and pedal glands, the rarity of territorialism and the tendency towards hierarchy and large size.

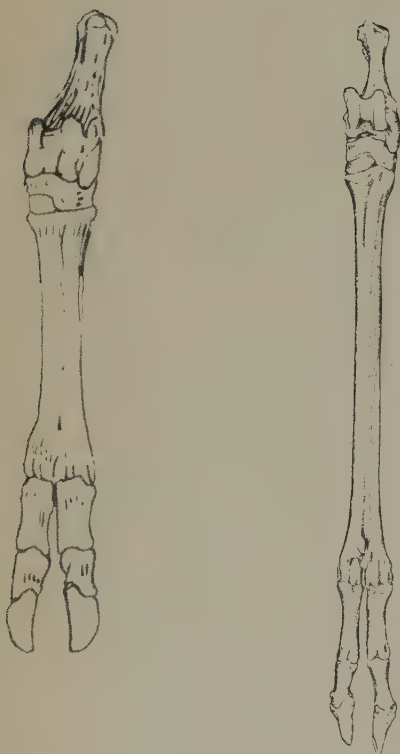
There has been a general agreement among taxonomists that three living groups can be assigned to the Bovinae—the cattle, the spiral-horned antelopes (respectively classed as tribes, Bovini and Tragelaphini in this work) and the Indian nilghai, *Boselaphus*, which has given its name to the Boselaphini, a taxon in which the chousingha, *Tetracerus*, is also normally included.

Tetracerus and *Boselaphus* share such primitive characteristics as brachydont teeth, long premolar rows, a flat basi-cranial axis and well-marked



Tetracerus

Hindleg of (left) bovine, *Bos* (right) antilopine, *Litocranius* showing differences in proportion and more developed articular surfaces in antilopine.



temporal ridges, features which are found in numerous Miocene bovid fossils from Eurasia and, to a lesser extent, Africa.

From this generalized boselaphine lineage Gentry (1978a) has envisaged the Tragelaphini emerging about 12 million years ago, while he has described the Bovini as large-sized Asiatic descendants of the boselaphines which are only recognized in African deposits at the end of the Miocene.

This interpretation accords with the fossil record and it is realistic to regard the fossil Boselaphini not only as broadly ancestral to the other members of the sub-family but as the most ancient lineage of the family.

The conjunction of *Boselaphus* and *Tetracerus* in a single taxon is therefore convenient but it artificially unites two survivors of the most ancient stock of bovids and it may imply a false phyletic unity.

It is no part of this work to overhaul nomenclature beyond that of the fauna being discussed, but it seems worthwhile to raise doubts. In this instance a well-established and convenient taxonomic arrangement might help to obscure the relationship between two major divisions of the Bovidae and confuse affinities in the bovine lineage because the ancestries of *Tetracerus* and *Boselaphus* are likely to have divided long before Tragelaphini and Bovini became recognizable entities.

The chousingha may therefore occupy a position in relation to the Bovinae that is analogous to that of the neotragines in relation to the Antilopinae and this conception is given graphic expression on p. 8.

The fossil record reveals that a variety of extraordinary structures evolved on the upper skull surfaces of early pecorans. Initially serving as protective bumps, lumps, antlers, hairy or keratinous horns, these devices eventually became weapons of offence. Like the impermanent sheaths of the prongbuck and the occasionally sloughed stubs of the nilghai the four horns of the chousingha are surviving relics of a late phase in the extended experiment that preceded the evolution of typical bovid horns.

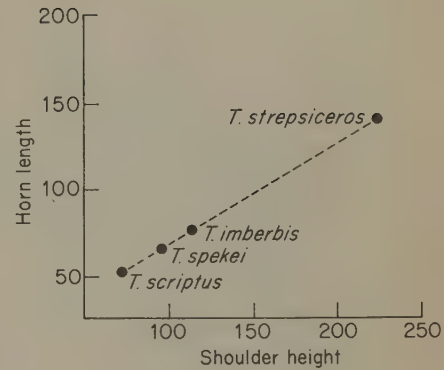
The smooth cones of Bovini and the keeled spirals of Tragelaphini are discussed in the relevant profiles.

Sexual dimorphism in the Bovinae takes various forms. Commonly explained as the product of male competition, sexual dimorphism in size and weight has, indeed, just been discussed in these terms. However, male monopoly in the possession of horns or in peculiar colouring may be subject to different selective pressures. On p. 44 I suggested that hornlessness may be as much the product of female strategy as of male competition. On p. 340 I suggest that more conspicuous colouring of males does not only advertise and provide a focus on specific characters. In some highly social antelopes, both bovine and antilopine, improved discrimination between males and non-competitive classes may be beneficial, because cows and calves are not caught up in the energy-wasting competition of mature males.

In the bovine species where males only are horned i.e. *Tragelaphus* there is some correspondence between horn length and shoulder height. This seems to reflect the simple "defensive shield" function of horns and reinforces the argument that successful defence is a major factor in the evolution of horns. This does not apply to bongo and eland where both sexes have horns, and there are more complex considerations (p. 82). Varied fighting techniques and horn shapes of Antilopinae obscure any size/length trend.

Much more needs to be learnt about temporal sequences and the relative frequency and intensity of male competition in antelopes before we can arrive at a well structured analysis of bovid spacing systems. It is already clear, however, that less complex horns in the Bovinae are symptomatic of less demanding, less complex spacing mechanisms than those of many Antilopinae, although large, social species in both subfamilies may have many similarities.

Increasing graminivory in Bovini, Alcelaphini, Reduncini and Hippotragini together with enlarging body size and greater sociality have wrought many convergences. We have seen how convergence had complicated efforts at defining bovid characteristics at levels higher than the tribe but there are overall differences. For example, a less testing, smaller range of habitats is occupied in fewer bovine species, of larger size, with slower gaits and less active life-styles, (manifested in the shallow sculpture of condylar surfaces at the hocks and fetlocks). A promising area of investigation could be tragelaphine "avoidance" a strategy that does not seem to have its equivalent among the Antilopinae and may be symptomatic of a fundamentally different male-spacing system. Further study should contribute to a better understanding of the primary bifurcation of bovinds.



Relationship of horn length to shoulder height in four species of *Tragelaphus*.



Oxen

Bovini

Genera

Syncerus

Bubalus (domestic)

Bos (domestic)

The Bovini are characterized by low wide skulls with a short face and smooth horns which tend to splay out sideways from the skull. Internal sinuses have developed at the base of the horn cores and there is considerable variety in the elaboration of bosses in living and extinct Bovini.

In spite of their superficial similarity the Asiatic and African buffaloes are not closely related, and an early relative of *Syncerus*, the relatively small, stub-horned *Ugandax*, suggests that each of these buffaloes evolved independently from very much smaller ancestors.

Syncerus has replaced a very long-horned buffalo, *Pelorovis*, which was very abundant from about four million years ago up to the end of the Pleistocene.

Several species of wild oxen have been domesticated. The wild ox or aurochs, *Bos primigenius*, had become domesticated in Greece and Asia Minor 8,000 years ago. In India, a quite distinct ox, the heat-resistant zebu, was already well-established 6,000 years ago. The banteng, *Bos javanicus* has a long history in Indonesia. In the hills and mountains of Malaya and India semi-feral herds of gayal, the domestic form of gaur, *Bos gaurus*, have always lived around the villages. In Tibet, the yak, *Bos mutus*, has been domesticated for about 3,000 years. The water buffalo, *Bubalus arnee*, has an even longer history of domestication in the tropical Oriental Region and was present in the Euphrates Valley in Assyrian times.

It is very unlikely that the diverse peoples of these regions all engaged in the active capture and rearing of five species of wild oxen. Consider instead what benefits are offered to man by this particular group of bovids and what characteristics they possess that might help to explain their early association with people.

Biologically rich localities must have been natural foci for human occupation from the earliest times. In particular, well-watered valleys could have supported larger numbers of people and allowed a relatively settled existence. The more vulnerable prey animals might soon have been eliminated around such settlements but large herbivores living in big herds are not easily deterred from rich and little-used pastures. Not only would herds of water-dependent wild oxen favour such localities but their numbers and behaviour need not have been greatly affected by moderate predation from humans, particularly if the hunters deterred or eliminated large carnivores.

An adult ox can feed many mouths for some days but there is as much skill in ensuring efficient use of such large beasts as in the killing of them, both require organized co-operative effort. In many choice habitats we can



Seal depicting a zebu, Mohenjo-daro
ca 2,500 B.C.

envisage people simply ignoring the wild oxen while easier foods were available, and some familiarity could be predicted in areas where the hunters' offtake from the oxen herds was small or infrequent and the oxen numerous.

Wild oxen are large, heavy and short-legged. They need long periods for rumination and the older animals tend to be slow and placid when not aggravated. In Uganda I have watched very small children playing within a few metres of the aged buffalo bulls that habitually graze National Park compounds and Ranger Posts.

Few bovids are better suited to function as living food stores than the tame, phlegmatic ox. It can be conserved to tide over lean periods or reserved for sacrifice during the ceremonies that punctuate even the most primitive societies' calendar. The ancient Celts sacrificed bulls during the August festival of Bron Trogrian and it has been suggested that English "park cattle" may derive directly from semi-wild herds left unmolested in sacred groves or parklands, where they could be kept for slaughter on ritual occasions. To this day gayal are only killed on special feast-days in parts of Burma and India and the herds live unattended near the villages.

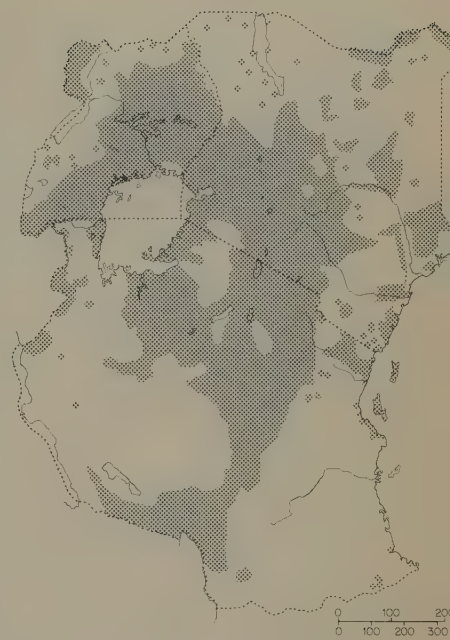
Most pastoral people in Africa get a significant proportion of their diet from wild sources or from primitive cultivation. They often need the special licence of a ceremonial sacrifice before consenting to kill their cattle. These precious animals are recognized as the ultimate buffer between themselves and the unpredictable vagaries of their environment and climate, but their normal functions are currency, bridewealth and the provision of milk.

The moment when men first milked cows was perhaps the beginning of true domestication and the boundary between well-managed familiarity and actual control might well have been marked by that crucial advance. However, the earliest origins of the association probably lie in a coincidence between man and beast in their habitats and deliberate exploitation of the natural characteristics of oxen.

A certain degree of ecological versatility and a generalized diet would have been essential pre-conditions for domestication. The flexibility of wild oxen can be illustrated by reference to the African buffalo. In Akagera National Park, Rwanda, Monfort (1979-80) studied two neighbouring buffalo populations. One tended to form large aggregations and exploit extensive homogeneous pastures by rotational grazing. The other population lived in a more diversified and dissected habitat. Smaller herds grazed in swampy valleys intensively during the dry season and on hilltop pastures in the rains but were highly fragmented and dispersed at other times. Monfort suggested that this naturally versatile exploitation of resources might serve as a model for effective livestock management in Africa.

Many pastoral peoples in Africa have in fact evolved ways of life that exploit the natural characteristics and ecological versatility of oxen. The annual movements of people and cattle have often been tested by centuries of practice. Some tribes actually leave their animals to forage unattended and the cattle may, like buffalo, scatter or aggregate according to the state of the range.

Until very recently Nation-States and the cash economy have been irrelevancies for societies that were almost wholly self-sufficient and had their own bovi-centric value systems. This is now changing, but it should



Cattle distribution in East Africa



■ Areas in which tse-tse fly vectors of human and animal trypanosomiasis are absent or have been eliminated.

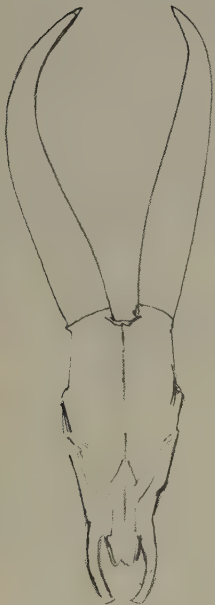
□ Distribution of tse-tse.

be remembered that even as the world changes around them, the proud and courageous pastoralists retain very real wealth in land and stock. The boundaries of their tribal territories may have been maintained at the point of a spear but they were largely defined by the needs of their herds and frequently constitute naturally self-contained eco-systems.

The pastoral subsistence economy, which depends upon reserved access to huge stretches of country has posed problems for national planners, agronomists and would-be ranchers. Policies that would introduce fences and individual land tenure have usually been opposed by pastoralists through leaders who sometimes carry considerable political clout. We can expect, therefore, that the ways which people have devised or will devise in future to exploit natural grasslands, oxen and other herbivores will continue to raise major social, economic and political issues in Africa.



Ox skulls.
Below: zebu of Kilari type.



Domesticated Cattle, Oxen (*Bos taurus*)

Cattle are the most useful of all bovids and probably have greater ecological, economic and political significance than any other mammal, domestic or wild. They are a source of livelihood for millions of people in East Africa and for the traditional pastoralists they will continue to be what they have been for hundreds of years—the only means of inhabiting and exploiting vast tracts of country.

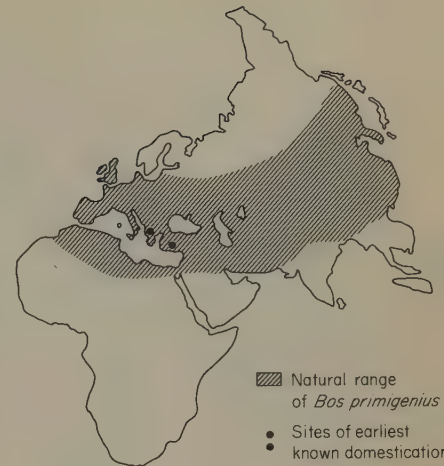
So fundamental are these marvellously adaptable and productive animals to peoples' existence that the interests of cattle, their owners and consumers are central and enduring issues in our social and political life.

I have already pointed out that cattle are a major factor in the biology of many wildlife species and that they are an element in the ecology of many African habitats. For wildlife biologists the cow serves as a yardstick for understanding other bovids. The physiology and anatomy of antelopes has been investigated by reference to the cow and, more recently, techniques borrowed or adapted from livestock management have been used to assess the productivity, turnover and relative efficiency of wild bovids. Many wildlife biologists have benefited from the vast literature on livestock and I suspect that all the writings on wildlife amount to but a fraction of this literature.

It would therefore be premature and pretentious to attempt any review of the place of *Bos* in the ecology of this region. However, this is not to accept the precedents of history and every practical consideration that wild bovids be viewed as little-known, poor relations of the cow. Instead, such a viewpoint is reversed in this volume.

The book has examined an indigenous fauna and its evolutionary past and from this perspective the cow is a very recently introduced exotic; in spite of the animal's importance no profile has been attempted.

Even while we acknowledge the adaptability, manageability and supreme economic value of this most remarkable of bovids it is worth remembering that *Bos* evolved in temperate environments and originally had a circumscribed geographic range. It is also worth remembering how tenuous and fragile are the human links that have extended this animal's ecological adaptability and geographic range.



Water buffalo (*Bubalus bubalis*)

Water buffaloes have been introduced into East Africa on several occasions but without conspicuous success.

The most recent introduction has been to the Entebbe experimental farm where they are reported to be doing well.



Syncerus caffer caffer.

**African
Buffalo
(*Syncerus
caffer*)**

Family

Bovidae

Order

Artiodactyla

Local names

Nyati, Mbogo (Kiswahili), Imboogo (Luhya), Mboho, Mbowo, Boo (Kichagga), Nyahi (Kirabai), Njari (Kuamba), Jowi, Jubi (Lwo), Odru (Lugbara, Madi), Soyot (Kipsigi), Soet (Kalenjin), Ekosobwan (Ateso), Losowan (Samburu), Olosowaan, Olarro (Masai), Gardas (Kiliangulu), Gessi (Somali).

African Buffalo (*Syncerus caffer*)

Races

<i>Syncerus caffer caffer</i>	Southern savannas
<i>Syncerus caffer mathewsi</i>	Bufumbira Mountains
<i>Syncerus caffer nanus</i>	Main forest belt

Measurements head and body

220 cm approx.

height

100—120 cm

tail

70 cm approx.

weight

270—320 kg (3 males)

265 kg (one female)

horns

30—75 cm

S. caffer nanus
(Forest buffalo)

head and body

240—340 cm

height

135—170 cm

tail

75—110 cm

weight

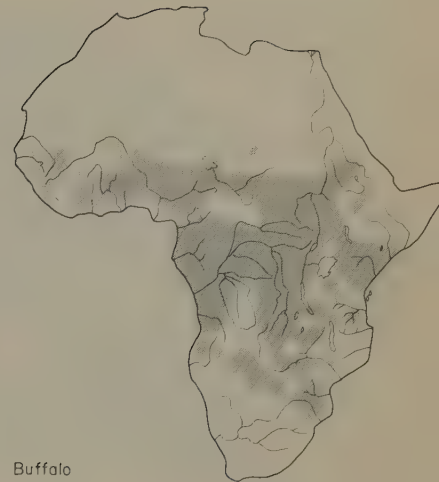
680 (410—850) kg males

480 (350—600) kg females

horns

50—150 cm

S. caffer caffer
(Cape buffalo)



Buffalo

The great black Cape buffalo bull with its curved horns and inflated horn bosses is such a spectacularly different animal from the much smaller red forest buffalo that this profile should begin with some discussion of the meaning of such differences within a single species.

The huge horns of the Cape buffalo are associated with a greatly increased sexual dimorphism (see measurements) and some interesting explanations can be suggested by relating the sexual and social behaviour of the buffalo to life in the forests and savannas.

Forest buffaloes live in habitats that are unsuitable to most of the larger carnivores and which offer an easy retreat into cover. Their heavy build, short legs and relatively slow pace are therefore no disadvantage. Because the buffalo is dependent on low-level browse and an undetermined minimum of grass in its diet, it is limited to those areas of the forest where edaphic or physical conditions encourage growth at low levels or to small grassy glades where the sunlight reaches the ground. Such conditions occur along river courses, in water-logged basins and in small clearings and it is in these situations that forest buffaloes are found. Such grazing grounds tend to be of restricted extent, so they are generally intensively used, and "buffalo glades", sometimes surrounded by elephant tangles, are immediately recognizable not only within the range of *S.c. nanus* but also of *S.c. caffer*. The humid forest climate supports almost continuous plant growth, which ensures that a small area will support a buffalo throughout the year and heavy grazing and browsing of that area can help to limit or at least delay the height of plant growth so that it remains within the animal's reach.



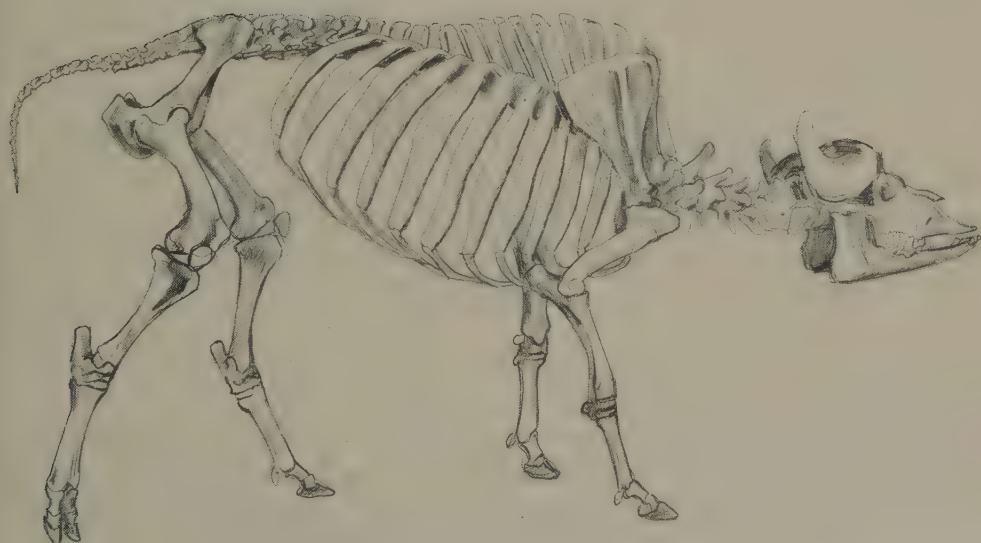
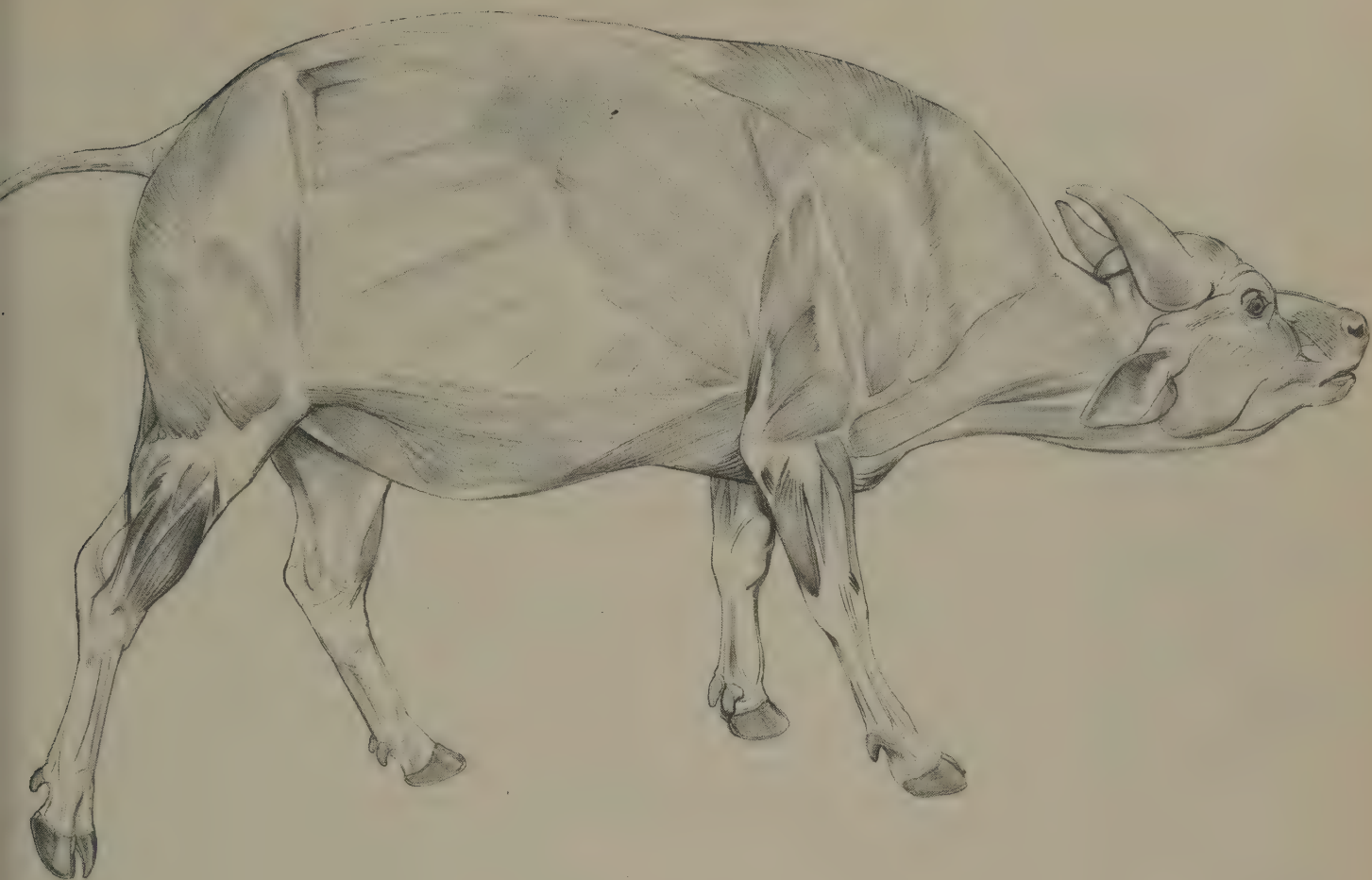
Savanna and forest buffaloes
(female).



Wild "hybrid" between *S.c. caffer* and *S.c. nanus*.

Where food is available in the forest it is in reliable, if limited supply, and there would be little incentive for long-range movements unless the number of buffaloes had outstripped their food resources.

Although the area over which forest buffaloes range has not been measured, they have been observed to be sedentary and tend to be found in small groups of two to ten animals (Happold, 1973), rising to 40 or more in favourable localities. In contrast, herds of 100 savanna buffaloes are common and average 350 on Serengeti, where as many as 2,000 animals have been seen together. The number of animals in a group of hierarchically organized animals directly affects the frequency of aggressive interactions and this might have particularly important implications for buffaloes, in which overt fighting is almost entirely limited to males, for the small number of adult males in forest herds would tend to reduce the number of challenges and confrontations. The smallness of the herds and their scattered distribution is also likely to have a conservative effect on the genetic make-up of the forest population. Conversely, dominant male types are likely to be selected for and have a greater genetic impact in larger herds, where dominance is tested against more challengers and with greater frequency. Any structural or behavioural feature that enhances a bull's breeding potential will tend to be passed on to a greater number of progeny, and it is this process that might have contributed to the enormous difference between forest and savanna buffaloes and might explain the apparently very rapid evolution of the latter population.

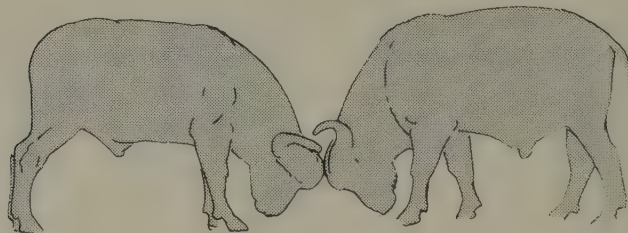




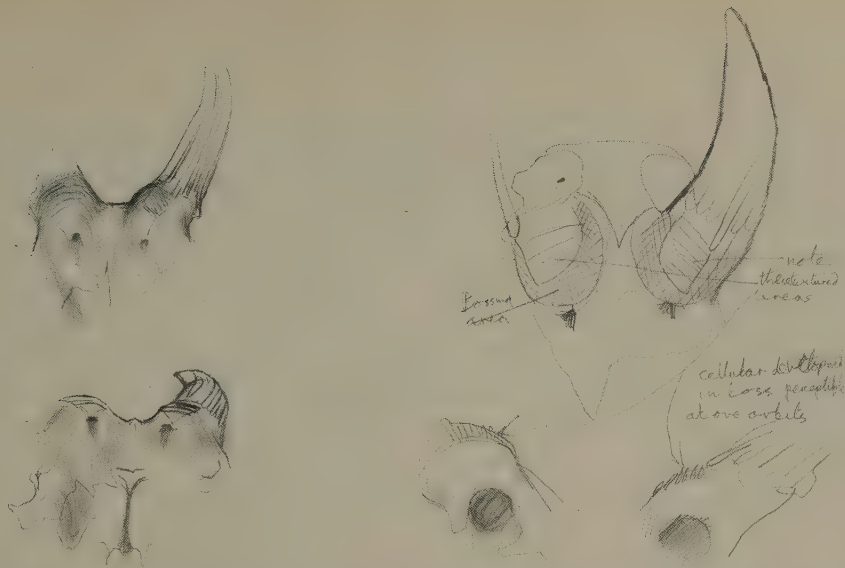
The savanna fauna of the Pleistocene is known from a wide scatter of sites across Africa, representing various levels or periods and a very diverse bovid fauna. *Syncerus* has been found at Melkbos in South Africa, at Omo in Bed IV, at Olduvai and in East Turkana, yet all the fossils found to date represent less advanced forms. Those from Beds B and G of the Shungura formation in Omo have a shortened braincase and strong temporal ridges (Gentry, 1978a), while *Ugandax gautieri* from the Kaiseo formation is, in Gentry's opinion, the earliest known member of the *Syncerus* lineage (see opposite). Even in the last Pleistocene Kibish formation at Omo a large *Syncerus caffer*, described by Leakey (1969a), has a close resemblance with the West African race, *S. c. brachyceros*, in lacking swollen horn bosses and drooping lateral hooks to the horns. Since the evidence suggests that the horns of *Syncerus caffer* developed the last two characteristics very recently, what explanation can be made for their very late development?

Bone and fossil deposits as well as numerous Palaeolithic rock paintings have revealed that another species of buffalo, *Pelorovis antiquus*, dominated the more open savannas and plains until very recently. Remains of these animals have been found in localities as wide apart as Algeria, Sudan, Ethiopia, Kenya, Tanzania and South Africa and they are quite numerous in East Turkana and some other deposits.

Although these buffaloes are thought to share a common ancestry with *Syncerus*, they resemble the Asiatic buffalo in the great span of the horns and the absence of bosses on the forehead. *Pelorovis* clearly had a different fighting and display technique to *Syncerus*. If the Asiatic water buffalo, *Bubalus arnee*, is any guide, the breadth of the span might have served to intimidate rivals long before contact was made, while each horn could be swung to strike a blow like a quarterstaff at close quarters; the greater the horn length the more momentum it gathered and the greater the reach. In this mode of fighting the blows would have been powered by the neck muscles. Some of the cave art represents animals with humped shoulders and thick neck and *Pelorovis* had longer legs than *Syncerus*. Apart from the implication of forest origins the shorter legs of *Syncerus* might be correlated with great weight and its fights are in fact a direct test of total weight and strength,



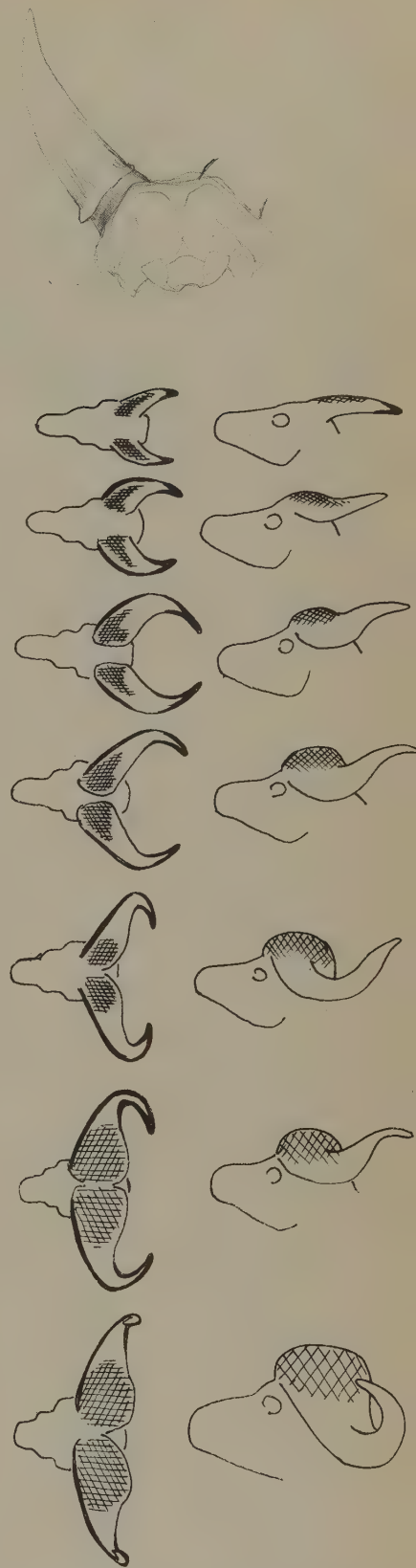
in that the animals push one another head-on or rush forward and clash foreheads. In fact dominance might have been tested by means of direct contact from a very early stage in the *Syncerus* lineage. *Ugandax* has raised bony striations that run across the swollen bases of the horns, suggesting



that this area was capped by some protective tissue that was distinct from the horn sheaths. The horn cores from Shungura have similarities with those of some *Syncerus c. nanus* specimens.

When contacts between animals are made at close quarters, as they tend to be in thick vegetation, there is less scope for displays and more likelihood of direct physical contact between conspecifics. The origins of forehead-to-forehead confrontations may start therefore in a constraint imposed by a closed habitat. If the large horn size of *S. c. caffer* can be correlated with increased male competition in the larger herds that can be supported by a more open habitat, there may also be differences in horn shape that are influenced by a widening of the visual field. The heavily obstructed and often swampy habitat of the forest buffalo would discourage headlong charges and it seems likely that this race would normally perform fairly static trials of strength in which the opponent attempts to push back or throw his rival. The shape of the horns is consistent with this mode of fighting, for in most individuals of *S. c. nanus* the upper surface of the horns is almost flat and their outer margins sometimes describe a figure as circular as a clutch-plate. *S. c. caffer* bulls adopt this method in addition to the usual ungulate rituals of circling, lateral parading and pushing. Sometimes they tangle the horns until a good purchase has been made and will then try to throw their opponent in a remarkably slow and deliberate manner. However, when the field is free from obstruction to movement and vision it is possible for a challenge to be taken up from a distance and end in a charge and head-on collision. The force of these clashes is such that an adult bull has been seen to be cartwheeled into the air and land on his back, and shattered horns are a commonplace amongst bulls. The momentum built up in a charge can be judged from an incident in Uganda in which a buffalo charged a man, missed him and broke its own neck against a tree trunk.

While I have already argued that the selective advantage for bulls with large horns might be correlated with an increase in the size of social units, the introduction of new elements into the buffalo's fighting style could also have influenced horn shape and it would be interesting to know more about fighting in *S. c. nanus*. A mere increase in the incidence of such behaviour could have contributed to the evolution of enormous horn bosses. The



Top: sketches of fossil *Ugandax* cranium. Margin: evolution of horn bosses in African buffalo from primitive *Ugandax* type.



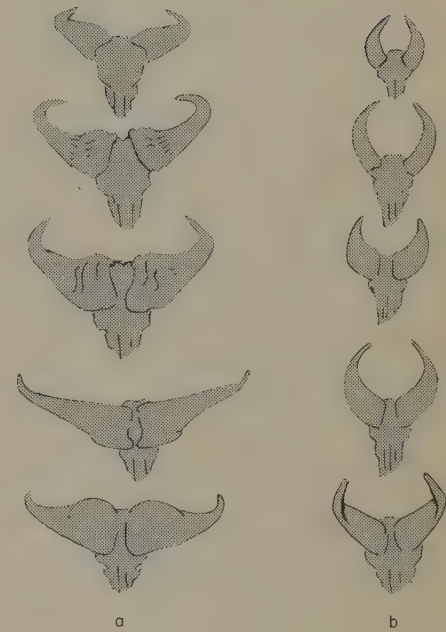
Distribution of *Syncerus caffer*
in 1975

massive inflation of the forehead region has been accompanied by a spread of fibrous horn growth up over the bosses in adult males, a sharp downward deflection of the middle section (in both sexes) and a vertical rather than horizontal hooking of the horn tip.

The social function of horns is not restricted to dramatic encounters between males. Like most ungulates in which both sexes are horned, all buffaloes jab and hook at one another in day-to-day jostling for space, food and water. While there is no evidence yet of a fixed linear hierarchy operating in large herds of females, the status or priority of individuals may be decided by small aggressive gestures, in which even the carriage of the head plays a part. The importance of these gestures may be reduced or an economy of effort achieved by the possession of especially conspicuous hooks or a broad span, since the sight of such weapons may be intimidating in itself.

A wide range of individual variation in both buffalo races and the existence of intermediate forms in West Africa together with fossil material allow a reconstruction of the evolution of horn shape to be made. The distribution and variation of African buffaloes has been discussed at length by Lydeker (1913a), Schwartz (1920), Christy (1929), Malbrant (1935), Schouteden (1945), Blancou (1954) and Grubb (1972). The map below and drawings opposite summarize the situation so far as it is understood today. The main division of *S. c. nanus* and *S. c. caffer* is an ecological one with the former in the main forest block and the latter distributed across southern and eastern Africa. Where the two come into contact, along the western Rift Valley, there are herds containing both races and there is abundant evidence of hybridization along this narrow belt, (the cow figured on p. 58 is a hybrid buffalo from the foot of Ruwenzori).

In the uplands of Kigezi and Ruanda there are distinctive "mountain buffaloes" that have been called *S. c. mathewsi*. In spite of its geographical locus wedged between the two major races, the fact that this population has consistent ecological and physical characteristics makes it less likely that these are stabilized hybrids. This area is the home of numerous relic and specialized populations, and these small, shaggy animals also seem to be adapted to a cold subalpine environment. On the basis of horn shape, *S. c. mathewsi* would seem to be intermediate between *S. c. nanus* and *S. c. caffer* and it is possible that this population represents a relic pocket of a form older and earlier than *S. c. caffer*.



Variation in horn shape in: a. *S. c. caffer*; b. *S. c. nanus*.



In the northern savannas west of Lake Chad the buffaloes are very much larger and are quite different from *S. c. nanus*. However, like *S. c. mathewsi*, this race, *S. c. brachyceros*, is also intermediate between *S. c. nanus* and *S. c. caffer* in horn characters, the arches being more divergent than in *S. c. nanus* and drooping slightly below the facial plane. On the other hand, the bosses are very poorly developed. There is an overlap between the dimensions of forest and savanna buffaloes in West Africa and Grubb (1972) suggested that *S. c. brachyceros* might have colonized the savanna biome independently following a phase of climatic change. He also offers the

alternative that *S. c. caffer* might have derived from a *brachyceros* stock. The existence of *S. c. mathewsi* and the occurrence of fossils resembling *S. c. brachyceros* in South Africa, Olduvai and Omo make the latter more plausible and suggest that these less extreme types of savanna buffalo were originally widespread. Perhaps they dominated the moister, more woody savannas and only gave rise to *S. c. caffer* as *Pelorovis* became extinct and so released its niche.

While the range of habitats occupied by *Syncerus* today is very great, the buffalo betrays its recent forest origins in a number of ways. For example, vision, which is the dominant sense for most open country antelopes, is of less importance to the buffalo than hearing, so much so that blind buffaloes which are otherwise fit and active have been found in buffalo herds. I have listened to buffaloes feeding in dense forest at night lowing quietly to one another, presumably keeping in touch by this means. Dependence on sound is appropriate wherever communication is obscured by vegetation or darkness but a nocturnal activity pattern can also be seen as simulation of the cool, dark conditions of the ancestral forest. Wherever they can, buffaloes seek forests or wet valley bottoms during the dry season and, in the absence of fresh green growth, they lose condition faster than most of the other savanna ungulates. Field (1972) found them sensitive even to small changes in the vegetation as it dries out and they are completely dependent on water. Although able to stand exposure to hot sun they conserve energy by remaining immobile, and solitary old bulls are particularly prone to spending very long periods of time in or near wallows, sometimes close to hippos that likewise use wallows for coolth and moisture and also as tranquil refuges where energy need not be wasted. The coincidence is not without significance, for while the dependence of these two species on water may originate in the swampy forest habitats of their ancestors, they are able to share pastures with species that are ostensibly much better adapted to hard times. One reason for this may be economic feeding habits, a feature that may also be related to forest origins as well as long resting periods. In the Ruwenzori Park, where buffaloes are of mixed savanna and forest ancestry, Grimsdell (1968b) determined that they only graze for an average of nine hours in the twenty-four, five or six of which are at night. Pienaar (1969b) observed that buffaloes are less destructive of the range than gnu or zebra and Vesey-FitzGerald (1969) has pointed out how the structure of the sward and quality of a pasture are improved by buffalo grazing.

“They apparently seek growth of a fairly lush nature. Having found this, the animals ‘nose’ their way forward below the more mature top growth, provided of course this is not too thick, and bite off the younger shoots. During this process, the fibrous culms tend to fall from the corner of the mouth if some happen to be bitten off. The ungrazed rough tends to be trampled down by the passage of the herd so that during future passage over the pasture it becomes easier for the animals to get at the new shoots. Furthermore the act of clipping the shoots stimulates further growth, while the trampled and discarded straw mulches the ground ... During subsequent visits to the pasture both the avoidance of less favourable places and the continued use of the more favourable places become an accumulative process and in this way a mosaic of grazed and neglected patches is produced.”

Species of star grass, *Cynodon*, are often dominant in buffalo pastures. This rapid-growing grass colonizes disturbed soil, soon forms a dense cover and suppresses other grass species. These characteristics are favourable for buffalo, as their broad mouths cannot separate grass parts or species and rapid growth encourages fairly continuous grazing. Another grass that maintains a dense cover in spite of heavy grazing is *Sporobolus*, and, depending on the habitat and the season, *Cenchrus ciliaris*, *Heteropogon*, *Digitaria* and *Panicum* have been recorded as important fodder, while swamp vegetation is often eaten in the dry season, notably *Leersia hexandra*, the shoots of *Cyperus laevigatus* and *Typha*. Conversely, there are grasses that are positively avoided, such as sword grass, *Imperata*, the coarse, narrow leaved feathergrass, *Aristida*, and the aromatic *Cymbopogon* spp. Browsing is probably of greater importance for *S. c. nanus* but Leuthold (1972) recorded that a third of the diet chosen by a hand-reared Cape buffalo in Tsavo consisted of dicotyledons. This animal accompanied two orphans, a rhino and an elephant, which might have influenced its choice of diet, for buffaloes normally remain close to their mothers up to the third year of life and probably acquire food preferences from them.

This long period of close dependence is very marked in buffaloes and is a conspicuous feature of rescued orphans, which become very dependent on their foster parent.

The mother-young link is both unusually intense and prolonged in this species and it probably provides the nucleus for social life. Grimsdell (1969) found that the female membership of herds is exceptionally stable and cohesive and Sinclair (1974b) thought that family grouping could possibly last throughout life. Small herds, which are commonest in forest and also in more difficult drier habitats, generally comprise at least one female and two or more offspring. Where there are several breeding females in close association this would not be inconsistent with their being closely related, as home ranges are of limited extent and there is no evidence of female progeny being expelled or prone to wander. In many of the National Parks where savanna buffaloes have been studied in recent years, protection from hunting and the absence of rinderpest has allowed the growth of numbers over a relatively short period and very large herds are common. In these circumstances a family lineage would soon lose its identity. Nonetheless, airborne observers have noticed a tendency for large herds to split into smaller groups when frightened and similar fragmentation takes place naturally each year during the dry season. Grimsdell (1969) saw intermingled herds separate out again with the same animals as before, so individuals must be able to differentiate members of their own group. To this end the voice may be an important means of recognition.

In the Ruwenzori Park herds average 100 individuals and their ranges overlap considerably. In this area with a yearlong abundance of food and water Grimsdell found that one herd confined its movements within an area of four square miles. Sinclair (1974a) put collars on individuals from separate herds and recorded their movements over a period of three years and he also mapped the position of all herds during each census. The marked buffaloes revealed that these larger herds also overlapped in range, particularly during the wet season, when they wandered more widely. A

herd was capable of travelling up to 30 km in 24 hours and the average home range was about 50 km in diameter. Very large herds of 350 animals or over were found to be spaced about 6 to 10 km apart. Since this distribution pattern does not correspond with that of the habitat, Sinclair suggested that the spacing of large herds could result from home-range behaviour and he stressed the role of family bonding in a group's attachment to a home range. This seems a likely explanation and, bearing in mind the expansion of buffalo populations in recent years, it is possible that the situation is the product of a preference for kinship-based associations. Any tendency for one family group to discriminate in its intercourse with other groups might lead towards polarities of this sort, particularly if older animals recognized and favoured associations with relations. Any tendency to avoid unrelated or least-related herds would have some effect in delimiting ranges and once a focus of activity had become well established it is possible that this home range could continue to restrict or inhibit the free distribution of buffaloes throughout the available habitat.

In spite of a continuous growth of numbers in his study herd, Grimsdell (1969) found that the female members were exceptionally cohesive and splits were very temporary and took place during the dry season (which are not very strongly defined in western Uganda). It would have been interesting to learn the long-term course of events, for ever larger groups eventually meet their environmental limits and it is likely that many smaller herds have their origins as splinter groups from larger ones. Sinclair has pointed out that the timing of the breakaway of male subgroups and of subdivision in the Serengeti herds is a direct result of dry-season fragmentation of their habitat. Extensive overlap of herd ranges may also derive from the splitting of units and the ease with which herds associate on common ground may also reflect this past. Association or re-association is easiest during periods of abundant food and water and the congregations of up to 2,000 buffalo that have been seen in Serengeti during the rains are only possible on a rich and well-watered range where there is minimal competition for resources and while the climate is temperate. The latter factor may be of crucial importance, because while it is probably unsuitable vegetation that limits the movements and herd size of forest buffaloes it could be physiological limitations and a need to conserve energy that restrict a savanna population during the dry season. This is most obvious in the old males mentioned earlier but they may simply reflect in an exaggerated way a trait that is of more general significance for the species. In all habitats the males join the female herds with the arrival of the full rains and their numbers tail off rapidly with the arrival of drier, hotter weather. In Uganda, the influx coincides with the mating peaks but this is not so further south, where there is a single rutting peak some months before. The number of males in the bachelor class therefore varies with the seasons, not with the rut, and estimates range between 3.9% and 15% of the population. The bachelors include two distinct age groups; young males about four to seven years old and males of twelve or more years. Grimsdell was able to show a decline in cell function in the testes as well as an overall loss of weight in the senile bulls and he also called some of the older herd bulls "incipient bachelors" as they became increasingly detached from the herd's activity.



Bulls are always at the rear of a frightened herd largely because they are so much heavier and in the end the price of sexual dimorphism and competition between males may be a contraction of the prime of life into a career of four or five years as a herd bull. After the age of about twelve it looks as if the best strategy to keep alive is to reduce activity to a minimum.

The short reproductive life of a buffalo bull implies a fairly rapid turnover of males within the herd and this factor could speed up selection, particularly if competition favoured characteristics that enhance dominance. In fact, competition does not normally take a conspicuous form and this is due to the establishment of linear hierarchies amongst the bulls (Grimsdell, 1969). While rank order gives priority, in mating this is by no means exclusive and an oestrous cow may mate with a succession of bulls (unlike the Chillingham cattle observed by Darwin in 1896). It is not clear to what extent it is the intolerance of herd bulls that drives newly adult males out of the herds, nor is it clear what the role of the mother is in this break, but male offspring do not remain attached to their mothers as long as females and at the age of about four years the young males tend to collect on the peripheries of mixed herds or in small bachelor groups. the seasonal movement of older males in and out of the breeding herds facilitates changes of herd allegiance and it is only the males that readily change herds (Grimsdell, 1969).

The large number of females in a herd and the inconspicuous or ambiguous nature of their interactions have made it difficult to demonstrate whether the ranking that occurs amongst the cows is linear or not. However, horns sometimes become entangled during sparring matches and a cow gives frequent expression to its seniority over its older offspring. Cows with small



calves are also more aggressive and other members of the herd avoid threatening them in any way (Sinclair, 1974a).

The protective behaviour of a mother towards her offspring and the close bonds that develop between them ensure that the beginnings of rank order lie in the subordination of the young to the mother, since dependence is protracted over a very long period and is largely exclusive of other relationships. This is illustrated by the persistence into adult life and into relationships between bulls of infantile appeasement behaviour. A subordinate animal approaches its superior with lowered neck and upturned chin and like a sucking calf nuzzles the undersurface of the dominant animal's body and then walks off bellowing. Another instance of an infantile trait serving adult ends is the calf's distress bleat. This call is of so great functional importance because very young animals may not be able to keep up with the herd and, on finding themselves left behind or in trouble, must recall the mother. Furthermore, the response to a bellow of distress is immediate and is not limited to the mother or to females alone. A very similar call may be made by any animal, male or female, young or old, when in difficulties and an entire herd in headlong flight will instantly halt and reverse direction if a harassed or wounded animal bellows.

Bulls and cows may reply with hoarse, strangled calls and the herd may rush up to the distressed animal *en masse* or make more hesitant advances and retreats with their heads and shoulders angled up into the air. (An exaggerated form of this alarm posture serves to deter attack from another male and has been described by Sinclair as a flight intention position.) Buffaloes have been seen trying to raise a wounded animal with their horns and there are numerous instances of buffaloes attacking predators. Even solitary bulls respond and will protect another male, but only if the animal makes a distress call. Cowie (1966) described an old bull tossing a lion into the air after it had attacked his younger companion, whereupon the victim, which had bellowed as it was pulled down, then joined the other bull in pursuing the limping lion. Beyers (1964) published photographs of a buffalo actually goring a lion. Yet the reactions of individual animals are variable, Schaller illustrated this with the contrast of a one-and-a-half-hour's battle



between a lioness and a young male buffalo (of which the lioness eventually tired) with the inexplicable emergence of an old male from his safe wallow into the jaws of five lions. Significantly, this animal bellowed but otherwise made no effort to defend himself. Had a herd been within earshot there might have been no need. "There were no violent actions, no frantic movements, as the buffalo rolled on to his back, and with one lion holding his throat and another his muzzle, died of suffocation. It was a scene of such impersonal force that it achieved an elemental beauty". (Schaller, 1972b).

While the response to a distress call is not restricted to adult females, the fact that females are normally in a herd ensures that its primary effectiveness lies in its being a herd-response. The security provided by a mother is coincident with the herd security and the unusually exclusive and sustained mother-young relationship is simultaneously social in that the mother behaves as a herd member. The herd is always a refuge for all females and younger males but even the loser of a fight between adult bulls has been seen to run back into the herd after he was wounded, much as a calf would. Such "big baby" behaviour reinforces the suggestion that the buffalo's social life is built around the links between mother and young. The presence of totally blind animals in herds has been mentioned, and another illustration of the security of herd life was provided by the appearance of a three-legged female in a Uganda herd. This cow had a completely healed stump below her left hind hock yet she was pregnant and in good condition. There are few antelopes that could survive such an injury because a predator would kill them.

Defences are so good in the buffalo that predation is normally not a major factor in population control. This fact has made the buffalo an interesting subject for studies in natural regulation of numbers. Studying two Uganda populations, Grimsdell (1968b) thought that both maintained stable numbers but the Ruwenzori Park buffaloes were five times as dense as the Aswa Lolim population because about five times as much of the habitat was suitable. He suggested that the regulation of numbers in both areas was adjusted to the level of food and noted a differential mortality





in the young. About half of the Ruwenzori calves survived their first year of life, whereas there was a 70% survival rate in Aswa Lolim, where mean herd sizes were smaller. Sinclair (1974a) also concluded that food was the principal regulator of the Serengeti population but he found instead that all classes were affected, although he noted slightly fewer young in smaller herds. During the driest times of the driest years dependence on water and their preference for riverine habitats lead to intense competition for food, both with one another and with other species.

In those areas where buffaloes form a significant part of the lions' diet, lions have little or no effect on the breeding rate because it is mainly the solitary males that are taken. For instance, Schaller (1972a) found that 88% of the Manyara kills were of this class. Apart from lions, packs of hyaenas and large crocodiles, few other predators can kill fully-grown buffaloes. Leopards and hyaenas will kill the occasional youngster if it has become separated or is unable to keep up with a panicked herd. However, this seldom happens as a herd tends to wheel round after an initial run and reapproach, since, like cattle, they are often intensely curious.

In most areas buffalo breed continuously but have well marked seasonal peaks. Grimsdell (1968a) found increased conceptions coincided with rising nutritional planes in the wet seasons so that there may be a biannual breeding pattern along the equatorial belt. South of the equator, where the dry season is more severe and the rains tend to coalesce, there is a single prolonged rut towards the end of the wet season and this too coincides with peak condition in the animals.

As a female comes into oestrus many males become interested in her urine and a succession of bulls may lip-curl over her urine or vulva. As her oestrus period proceeds the effects of male hierarchy come into play, for although a number of them may mate her, the top two or three bulls have priority (Grimsdell, 1968a). Copulation is preceded by close attendance and by repeated resting of the bull's chin on the cow's rump.

Gestation lasts approximately 11 months. The interval between calving and the next conception is variable. For example, Grimsdell found an average interval of 18 or 19 months between calves in the lush habitats of the Ruwenzori Park but about two years in Aswa Lolim, while Pienaar (1969b) thought that intervals of 18 months were possible under good conditions but that otherwise cows calve every alternate year in southern Africa.

Calves grow very rapidly in their first year and become sexually mature from about two years old. However, Wilson (1969a) and Pienaar (1969b) recorded first parturitions at the age of four to six years. Grimsdell has calculated a maximum life expectancy of about 20 years but zoo specimens have lived 26 years.

Attempts at domestication of the buffalo have mostly failed because they become intractable. Handreared animals of both sexes may remain very docile with their keepers when adult but can at the same time be extremely aggressive towards other humans. Because they have been implicated in the spreading of bovine diseases and in raiding cultivation and breaking fences, buffaloes have been eliminated from many areas in recent years. For example, over 10,000 were shot in Uganda in the four years following

Near full-term foetus.



the end of the Second World War, a period of intensive agricultural expansion. Nonetheless, they sometimes continue to survive in small numbers by becoming wholly nocturnal and lying up in inaccessible marshes or thickets during the day.

The horns are very popular symbolic trophies. As whole heads mounted on shields, or as sheaths, carved and stuffed with vegetables, earths and bits of animals, buffalo horns serve the common purpose of symbolising virility or fertility. In Buganda they are known as *jembe* in traditional witchcraft, being regarded as an appropriate home for the *mayembe* spirits which influence the success of both procreation and the harvest and so buffalo horns are a common artefact in the paraphernalia of witchcraft. However, witches and diviners do not compete over the size of their horns in the way the trophy hunters do.

Three buffaloes showing extremes in elevation (left); bossing (middle); and drooping (right) of the horns.



Tragelaphines

Tragelaphini

Genera

Tragelaphus

Boocerus

Taurotragus



The tragelaphine antelopes are medium to large antelopes with deep bodies, long necks and legs, narrow heads with big ears and twisted or spiral horns. Their teeth are low-crowned and, like their digestive systems, are adapted to a diet of soft, nutritious vegetation and fruit, which is gathered by what could be called a “gleaners’” strategy.

They have slow tentative gaits, adapted to reduce their conspicuousness and their elegant, relatively unmuscular limbs are poorly adapted for much more than a short rush for cover. Only the more powerfully built elands are endowed with any stamina; the other tragelaphines prefer to freeze, slip quietly away or crouch when disturbed.

The colouring of tragelaphines is also appropriate not only to the “lying-out” phase in calves but to crypsis in adult life as a major strategy for escaping predators. All species have stripes on reddish, brown, fawn or grey backgrounds with very similar flash markings of white and black on the legs, throat and head. Populations of sitatunga, bushback and eland in the eastern and southern parts of the continent, where habitats tend to be drier and colder and the animals are thicker coated, may be nearly or wholly stripeless in spite of the western subspecies being well striped in both sexes. If striping was only related to crypsis exceptions to such a general tragelaphine rule would have to be exempted or relieved from some of the selective forces favouring this pattern. For eland calves, which emerge from lying-out after only two weeks, the subsequent protection of the herd could influence their stripelessness, in which case the faded striping of the no less protected eastern elands must be regarded as vestigial. On the other hand, the correlation with thicker coats is meaningful and, if the undoubted utility of lines to enhance camouflage has acquired a secondary social role, then more complex factors may be involved. Long hair should actually enhance the camouflage effect of white lines by mottling and breaking them up but, if they function in any way as an intra-specific signalling device, then this function could be undermined by reduction in their visual clarity.

If stripes represent an elaboration of infantile blotches, their communicative function might lie in the young one’s relationship with its mother. This is, after all, the only sustained association common to all tragelaphines. What could the stripes’ role be? All tragelaphines employ broadside displays in coercing or imposing themselves upon another animal and the earliest manifestation of this is the young one halting its mother’s movements by standing broadside in front of her. Camouflage is designed to fool predators but it could have the rather undesirable effect, if not of fooling the mother,

Above and opposite: lesser kudu.
Tragelaphus imberbis.



of diluting her visual responses. Tragelaphines are highly visual animals, relying more on sight and sound than most antelopes. They have a poorly developed olfactory system and can ill afford to reduce the utility of visually-based communication. Optically, light blotches are probably more effective as camouflage than stripes but close up the latter should make a more distinctive visual impression, because some neurones in the visual cortex are known to be programmed for linear orientation, contrast and edge effects (see Vol. IIIB, p. 135). Transformation of blotches into lines might therefore be a modification of camouflage that, at close quarters and in appropriate circumstances, transforms the tragelaphine calf, (or adult), into a highly distinctive display panel. Rangy flat-sided figures and the evolution of crests or manes enhances this mode of display. Its origins might therefore lie in a cryptic infant asserting its physical presence upon its mother and, by extension, upon other conspecifics. The tragelaphine lack of facial scent glands may be correlated with their non-territorial social system. Allsop (1971) has pointed out that, if long-spiked horns were used by tragelaphines in the sort of territorial contests that are normal in some other antelopes,

they would result in frequent deaths, and he considered that this horn shape is inappropriate to territorialism. It might be added that the prolonged expenditure of energy to be seen in alcelaphine and reduncine territorial males is unconceivable in tragelaphines, which are not built for such tests.

Male antelopes that are not preoccupied with territories are probably less exposed to predators, and Allsop (1971) saw the lack of territories in bushbuck as an adaptation to avoid predation. Comparing the ratio of lion and leopard kills with the prey species' relative abundance, Pienaar (1969a) estimated the "preference rating" of various prey species in the Kruger Park. Kudu and bushbuck were less heavily preyed upon by lions than two antelopes of equivalent size, the waterbuck and impala, but the leopard took more bushbuck than impala. The eland, on the other hand, was more vulnerable to lions than, for example, roan antelope.

PREFERENCE RATINGS FOR THREE TRAGELAPHINE AND
NON-TRAGELAPHINE PREY SPECIES IN KRUGER NATIONAL PARK,
SOUTH AFRICA (after Pienaar, 1969a)

Tragelaphine species	Relative abundance	Pref. ratings		Non-tragelaphine species	Relative abundance	Pref. ratings	
		Lion	Leopard			Lion	Leopard
Greater kudu	2.9	3.8	1.0	Waterbuck	1.7	6.0	2.2
Bushbuck	1.4 (est.)	0.2	2.7	Impala	53.7	0.4	1.4
Eland	0.3	2.0	0.6	Roan	0.2	1.6	0.2

Predation may also determine a gradient in group size which has some correlation with body size in that the larger the animal the more difficult it is to hide and the greater the benefits of social life. Large associations of bongo and eland can be correlated with the presence of calves but not with feeding conditions, and protection of the young is probably the principal reason for these associations and also may explain the acquisition of the horns in the females of these species; (even so, juvenile mortality is heavy in all species of tragelaphines). The mechanism drawing the animals together differs in emphasis between the two species. Female bongo associate with neighbouring females both before and during their calves' prolonged "lying-up" phases, whereas juvenile eland, which emerge from isolation at two weeks of age are spontaneously sociable with other calves and provide a focus for their defence by the entire herd.

Vision and hearing are well developed while scents play less of a role than in other antelopes. All species make loud barks, which probably act primarily as an intraspecific avoidance signal but might also serve as warning in some species.

Visual displays are very highly developed, particularly during male to male encounters and, to a lesser extent, in courtship. Dominant animals raise the head and chin, inferiors lower both, but either animal may tilt the head, thus displaying the horns.

Dominance displays are sometimes elaborate, sometimes very casual, I have noticed as many as six male bushbuck feeding together at one time.

A perfect gradation in the length of horns provided evidence for a linear hierarchy that might have helped explain their pacific relationships.

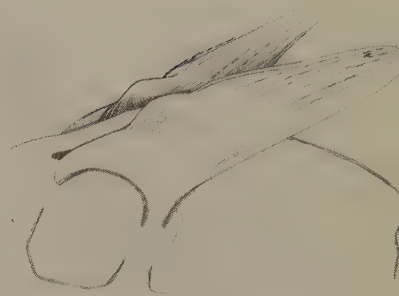
An established hierarchy would change slowly in species where male growth is very protracted, as it seems to be in several tragelaphine species. In fact, there may be a turnover in dominance because, on the evidence of captives, males seem to be subject to androgen cycles that render individuals extremely aggressive for relatively short periods. In most species the main function of the spiral seems to be to provide surfaces for the contestants to engage against in horn wrestling matches. The more elaborate the spiral the more ritualized the engagement.

The spiral form of the horns is the product of tensions exerted by the horny sheath upon the traverse of an otherwise straight-forward "core" inside. (There is no visible evidence for the bony material within the core travelling at different rates, which is an alternative explanation.) Differences in growth rate are obvious in the horn sheath because, as in bird feathers, periodic "hunger traces" tend to show up very readily producing lines of incremental growth encircling the shaft (well-fed captives may lack these groove traces altogether). Extra keratinous material is laid down along two narrow longitudinal zones. The first is simply an angle formed between two plane surfaces immediately behind and above the orbit, this "keel" follows the line of the post-orbital bar up along the shaft of the horn and it is only conspicuous in some tragelaphines. The second ridge of keratin is conspicuous in all tragelaphine species and emanates from a point well to the fore of the main shaft and just behind the supraorbital pits. In a young bongo these points are marked by distinct bony prominences which acquire a special significance when the evolutionary history of the tragelaphines is taken into account, because they can be usefully characterized as the vestiges of supplementary horns. These have amalgamated with the main horn but represent distinct sources of keratin with their own rate of growth, which is slower than that of the main shafts.

Within the first few months of growth a young tragelaphine horn reveals that the ridge of keratin drags back growth in the rest of the horn because of its greater mass and slower growth. At this stage the horn core is straight and pointed but the impediment of the frontal ridge forces the thinner but faster growing horn sheath to slew round the main shaft.

How soon and how much the horn begins to spiral depends upon a very limited number of variables. Since it is the sheath that imposes the spiral, (and creates an anticlockwise torsion from the base upwards on the right sides) its thickness relative to the diameter and length of core is critical in determining how much and how soon it begins to distort the traverse of the core. A thick core is not easily deflected by a thin sheath, whereas a thin core with a thick sheath is easily dragged into an open spiral.

The relative tightness or openness of the spiral is determined by the amount of material laid down by the frontal ridge. The post-orbital keel also influences horn shape, particularly in the "bladed" species, sitatunga, bongo and bushbuck. Here the growth is also held back so that there are two points of equally slow growth with a flat plane between them. The centre grows faster than its margins but the plane tends to slew round the axis of the shaft as a unit and the resulting reinforcement of the horn clearly



Horn cores of a young male bongo to show possible separate origins for keel and main shaft elements.

Bongo horn, showing role of differential growth in creating a spiral. Left: curved shaft, even growth shown by relatively straight growth ridges. Right: reverse view of horn with faster growth line on flat plane while retarded growth is implied by the kinks lying over the two heavy horn ridges or keels.

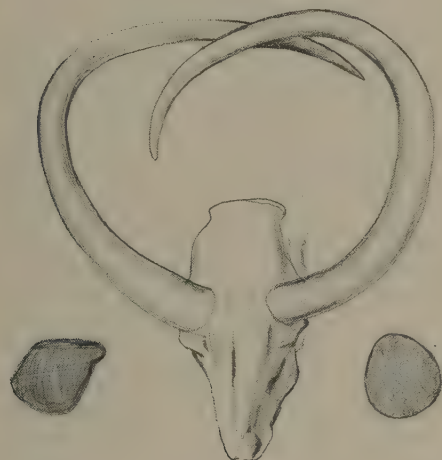


Greater kudu, *Tragelaphus strepsiceros*.



lends it exceptional strength. One other factor that might exert some influence is the relative speed of growth.

The form of all tragelaphine horns and possibly those of the various races of markhor, *Capra falconeri*, can be understood as the interaction of these few variables. In all species the thinner and longer the core the more pronounced the spiral. The variance in horn traverse is least in the "bladed" species and greatest in the kudu, where the shaft is more circular in section and the frontal ridge exerts a stronger influence. Thus the thick-sheathed, thin-shafted horns of the greater kudu become huge uninhibited corkscrews, while the thin-sheathed eland has a heavy frontal ridge twining tightly around a nearly straight thick shaft. The horns of Derby's eland are intermediate between those of the kudu and the common eland and show much variation in shape. Common eland occasionally develop exceptionally long and slender horns, particularly the females. When this happens a more open spiral, like that of a kudu, may reassert itself as can be seen in a female photographed at Ngorongoro in 1966 (see above). Fossil greater kudu show very considerable variation in the form of their spirals (see p. 79).

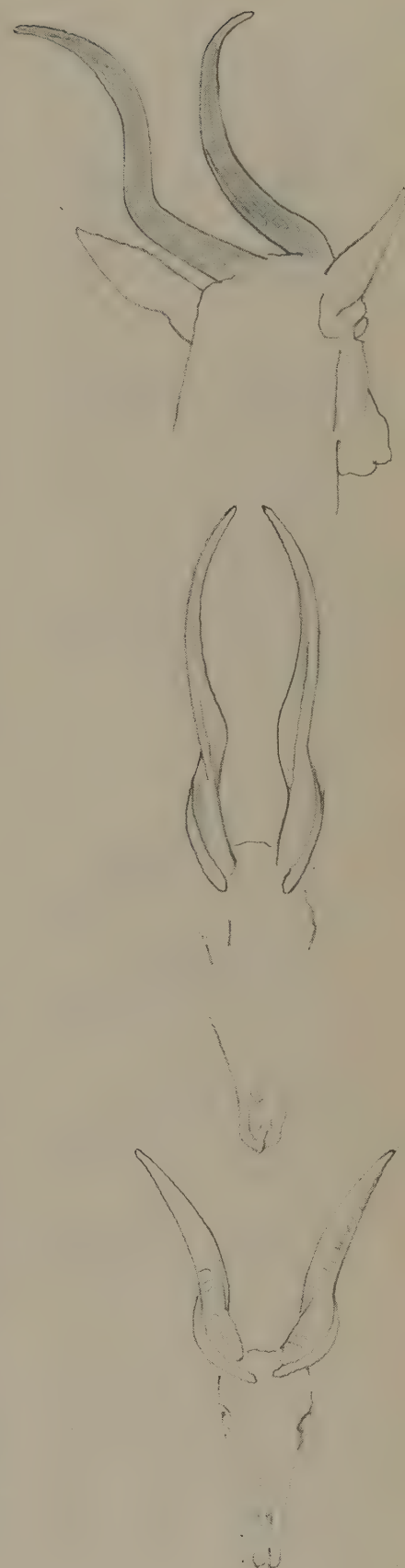


Text drawing: greater kudu, aberrant growth pattern—lacks ridge and has almost circular section and smooth surface; left: normal horn cross-section; right: cross-section in this specimen.

Margin: spirals in *Taurotragus oryx*.
Top: female eland with lyrate horns in Ngorongoro, 1965-66.

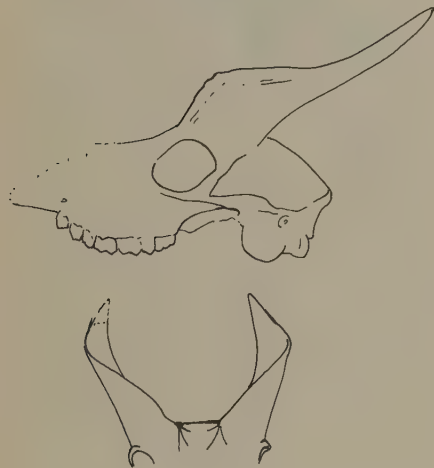
The role of the frontal ridge in determining the open spiral of a kudu's horns is dramatically exemplified when it is absent. The horns of a greater kudu skull in the Kenya National Museum (OM 1765) are smooth surfaced and nearly circular in cross-section. Lacking any trace of a frontal ridge they describe a broad semicircle which lies more or less in one plane. Presumably the supplementary horn buds were missing in this animal due to some genetic shortcoming (some individuals of the four-horned chousingha, *Tetracerus*, only have two horns). Similar horns have been seen in a female eland.

This aspect of the group's anatomy has some relevance not only for understanding the shape of their horns but also for their taxonomic affinities and evolutionary origins. In the oriental chousingha, *Tetracerus*, males normally have four horns instead of two and an extinct South African boselaphine antelope, *Mesembriportax*, appears to have had such prominent anterior keels that Gentry (1978a) considered that the horn sheathes might





North American antilocaprines. Left: *Illingoceros*; right: *Tetrameryx*.



Protragocerus labidotus.

have actually bifurcated like a pronghorn. A similar but less extreme separation of keel and shaft occurred in *Protragocerus labidotus* from the East African Miocene at Fort Ternan. Gentry (1978a) places this species close to the root stock of all Tragelaphini (see margin drawing).

The link between boselaphines and tragelaphines is close. Not only does the living *Boselaphus* resemble *Tragelaphus* in tooth structure, cranial and post-cranial anatomy but even its coat markings on head, neck and legs are uncannily similar. Moreover, the most telling links are fossil ones and they concern the Pliocene *Selenoportax vexillarius* of India, which is classified as a boselaphine but Gentry and Gentry (1978) considered could be as easily related to the Tragelaphini or the Bovini. This antelope has strong similarities with the Pliocene *Tragelaphus nakuae*, which is so like the bongo it was until recently classed as one, *Boocercus nakuae*. Earlier, in the Pliocene of Afar, there appears to be a species ancestral to *nakuae* (Gentry and Gentry, 1978) but even this fossil is less old than the many scattered fossils of *T. spekei/angasi* type which span a period of over five million years.

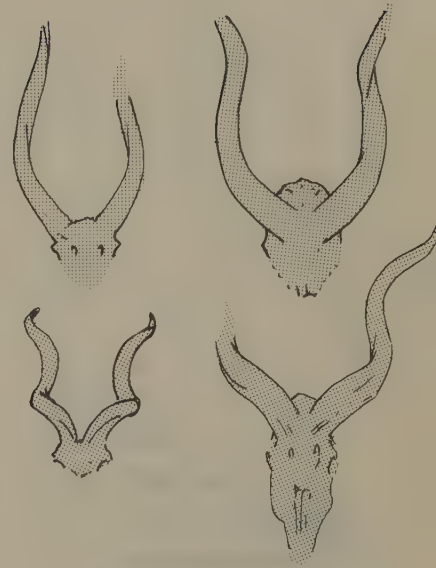
The tragelaphine radiation probably began with the ecological divergence of an ancestral stock common to *T. nakuae*, *T. spekei* and *B. eurycerus*. In all but its specific adaptations to swamp dwelling the sitatunga probably represents the most conservative form. It is a survivor living in a difficult marginal habitat by virtue of these minor adaptations. Anatomically it can scarcely be told apart from the nyala, *T. angasi*, which must have made even more subtle physiological and ecological adaptations to the semi-temperate and localized conditions of the South African cul-de-sac in which it lives. A continuous supply of leafy growth and year-long cover at low levels are the prime requirements for almost all tragelaphines and this the swamps provide in superabundance. Outside such specialized habitats these requirements are more easily and universally met for a small animal. The smaller the body size, however, the more intense and direct is competition from more advanced or more active bovids and other herbivorous animals and this particularly limits how small a tragelaphine can be. In spite of a modest consumption tragelaphines are slow movers and slow feeders and they can best survive in areas where the food is scattered and bitty, so that the pressure from predators and competitors is relatively light. In the less specialized habitats tragelaphines would be under pressure to narrow their "gleaning" niche and improve their competitiveness. At this end of the ecological spectrum the tragelaphine success story is the bushbuck, which may be a small-scale descendant of the same lineage as the bongo. Just tall enough to reach a higher feeding zone than many of its competitors, its nutritional needs are sufficiently modest for it to survive (at low densities) in areas of seasonal food-shortage. In more favoured habitats, its social system can allow a high density (up to 26 per sq. km) of evenly scattered individuals. At a subjective level its more robust build and more alert, active movements and demeanour imply that the bushbuck is an improvement on the sitatunga, but it might be worth making direct comparisons of various ecological and behavioural parameters to quantify this.

The bongo may be the large-scale representative of an early ecological radiation by the tragelaphines. Anatomically it resembles a heavy-weight sitatunga but like the bushbuck it has made refinements in its behaviour

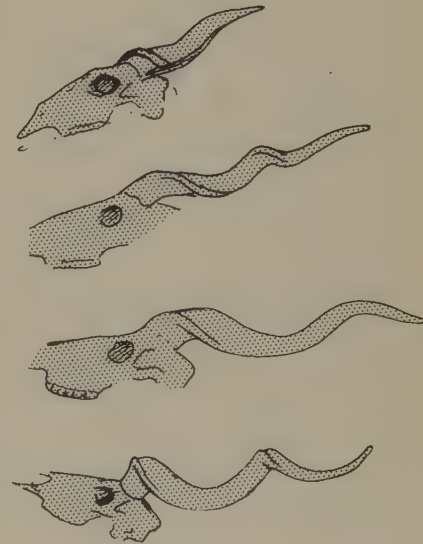
and ecology that are described in the species' profile. Whereas the bushbuck can support itself in areas with marked seasonal changes, the very much larger and more social bongo requires its more substantial dietary needs to be met throughout the year, and a climate capable of this tends to tie up primary production in wood and high canopy foliage. Seasonal movements may ease the difficulties but these sorts of limitations have probably meant that once a large-sized tragelaphine entered this niche its populations were of necessity small and scattered and the bongo's ancestors are likely to have entered an evolutionary backwater at a relatively early stage.

Like some other African mammals with origins in the moister woodland and forests, the tragelaphine pathway of advance has tended to lead out into the drier bushlands and savannas. (See Vol. I, pp. 60—77, 308—315; Vol. IIA, pp. 152—225; Vol. IIB, p. 420; Vol. IIIA, p. 310.) Scattered throughout the arid zones there are valleys or rocky outcrops where moisture is conserved, where evergreens and herbaceous growth can survive through the severe dry season and where the tragelaphines can expect to glean successfully around the year. These vegetation nuclei provide dry-season havens for the lesser kudu, the equivalent of an arid-adapted sitatunga or bushbuck. A vertical increase in the feeding zone is implied by the lesser kudu's very slender, tall proportions. Gentry and Gentry (1978) regarded *T. gaudreyi*, a common fossil from the late Pliocene (margin), as a possible ancestor for the lesser kudu, and the species is also close to the common stock of greater and lesser kudus. It has closely-spiralled horns which, like those of the sitatunga, emerged from the skull at a lower angle than either of the modern kudus (see margin). The greater kudu appears in the fossil record for the first time in the early Pleistocene in a form slightly smaller than the living species, *T. strepsiceros maryanus*.

The fossil skulls of kudus with horn cores that were 10—20% larger than those of the living *T. strepsiceros* are common in Bed II at Olduvai and Koobi Fora; appropriately sized teeth are also known from South Africa (Gentry and Gentry, 1978). This variety of kudu, *T. s. grandis*, belonged to an assemblage of animals that included many giant forms. These fossil remains belonged to animals that were altogether larger so that the greater horn size was probably proportionate. Their horns present an extreme in length and also of the trend towards an open spiral, which in other tragelaphines has been modified, progressed less far or been reversed. The fossil series suggest that both the body size and horn spiral of the greater kudu evolved along an ever-increasing and probably closely correlated gradient, until it reached its extreme limit in *T. s. grandis*, in an animal perhaps over 400 kg in weight and about 160 cm at the shoulder. The huge size of *T. s. grandis* would have demanded an extensive foraging area with the likelihood that a wider range of habitats would have been embraced. Even if the species occupied then the relatively narrow ecological niche it does today, which is very unlikely, its habitat would have been much more extensive because in the Mid-Pleistocene fire did not play the dominant role it does today. Populations would have been more widespread and more numerous, a conclusion supported by the abundance of fossils about 1.3 million years ago, at which time they were apparently a dominant large ungulate.



Top left: *T. nakuae*; top right: *T. gaudreyi*; bottom left: *T. imberbis*; bottom right: *Tragelaphus strepsiceros grandis*.



Changing shape and orientation of the horns in (bottom to top) contemporary *Tragelaphus strepsiceros*; Pleistocene *Tragelaphus strepsiceros grandis*; *Taurotragus derbianus*; *Taurotragus oryx*.

Even today kudu use the ecotone between bush and more open habitats and they are seasonally attracted into the open by an abundance of forbs or new flushes of herbaceous growth. The principal limitation on further expansion into open habitats is less a matter of dietary resources than its vulnerability to predators. Because of its size the giant kudu would have suffered from fewer predators. Furthermore, if the females had horns and were prepared to use them, then giant size could have helped emancipate this race of kudu from the major limitations that restricted tragelaphines to closed habitats. Since females of the greater kudu occasionally bear more slender, shorter and less spiralled horns, the acquisition of this trait in a savanna-dwelling population of giant kudu is quite feasible.

This modelling of the giant kudu's ecology is not prompted by the fossil's curiosity value. All the major adaptive features of the two species of living eland can be derived from a kudu and more specifically from a giant kudu, and the pre-eminence of *T. s. grandis* at levels just below those in which the first eland *T. arkelli* appears is significant. Elands did not evolve from the rarer bongo lineage, as has sometimes been suggested, but emerged from a much more widespread and dominant population that was pushed up against a traditional tragelaphine frontier.

What can a comparison of the two species tell us about the nature of the eland's transformation? The dietary changes are subtle but significant. Records of the plants taken by kudu and eland in an area of overlap in Shinyanga (Harrison, 1936) demonstrated some important trends, (in spite of uneven samples from a total of less than 800 feeding records).

A COMPARISON OF SOME IMPORTANT FOOD PLANTS TAKEN BY KUDU AND ELAND AT SHINYANGA DURING THE DRY AND WET SEASONS (from Harrison, 1936)

Food Species	Dry		Wet	
	Kudu n. 374	Eland n. 77	Kudu n. 122	Eland n. 177
<i>Abrus schimperi</i>	2.4	5.2	7.4	4.1
<i>Combretum</i> spp.	17.9	26.0	5.7	7.4
<i>Grewia</i> spp.	3.2	3.9	5.7	12.0
<i>Hymenodictyon parvifolium</i>	1.9	—	7.4	5.0
<i>Acacia</i> spp.	4.5	—	—	—
<i>Markhamia acuminata</i>	4.8	3.9	12.3	4.6
<i>Cadaba adenotricha</i>	10.7	—	—	—
<i>Cassia</i> spp.	14.7	3.9	1.6	2.3
<i>Thylachium africanum</i>	9.0	6.5	—	—
<i>Commiphora</i> spp.	0.3	11.7	0.8	7.4
<i>Sclerocarya</i> (fruit)	0.3	7.8	—	2.8
<i>Sterculia tryphaca</i>	—	—	5.7	8.7
<i>Ipomaea</i> spp.	0.3	—	10.6	8.7
<i>Vigna triloba</i>	—	—	9.8	6.9
<i>Commelina africana</i>	3.5	3.9	0.8	9.2

Percentages are of numbers of times a plant was recorded being eaten by each species in each season.

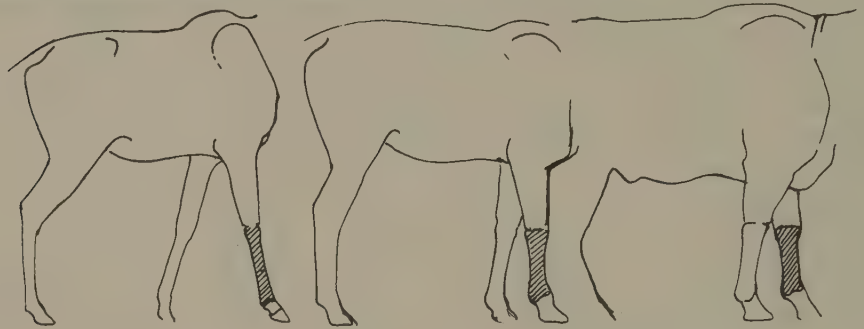
Many of the dominant species, *Abrus*, *Combretum*, *Grewia* and *Markhamia* are major items in the diets of both species throughout the year. They both have similarly varied diets during the wet season, including common ephemerals such as *Ipomoea* and *Vigna triloba*. Differences become more apparent in the dry season. Both species eat *Thylachium* and both feed on plants that are ignored during the rains but the kudu maintains variety spread over 25 species. The eland's diet is instead more restricted with 57% of its recorded feeding coming from only five plants out of 21. The kudu's foods are more scattered but they are of better quality than those of the eland and this is consistent with structural differences in their digestive systems. Comparing their stomachs, Hofmann (1973) classified the kudu as a folivorous "concentrate selector", whereas the eland is an "intermediate" or "mixed" feeder. The eland has remarkable variations in the mucosa of the rumen and the reticular crests, which imply greater adaptability than the kudu to seasonal changes in diet; the unique structure of the eland's omasal mucosa might signify a water-saving mechanism.

Habitat parameters for the two species have been compared by Underwood (1978) in a small South African reserve where the animals were artificially constricted around a dam. However, the Loskop dam reserve had been surveyed and mapped for soil fertility, and the record of sightings showed that while the eland used low nutrient areas somewhat more than the more fertile ones (56%), the kudu tended to avoid the former, 69% of the sightings being in high nutrient areas. The eland showed an 86% preference for the more open habitats, (*Protea* scrub, *Combretum* savanna and areas of *Diplorhynchus* and *Loudetia*). The kudu spent their time equally in the more open and denser surroundings and spread themselves through all the vegetation types. They were on steep hillsides as frequently as on lower slopes, whereas the eland were seen 69% of the time on flats or gentle slopes.

KUDU		ELAND		Vegetation and soil	
Hillsides			Dense vegetation	Soil nutrients high	
138		49			
Flats					
55		72			
Hillsides			More open and grassy		
23		89			
Flats					
89		399			
95		69		Dense vegetation on hillsides	Soil nutrients low
Hillsides			More open and grassy		
29		235			
Flats					
64		474			

Kudu-eland habitat preferences
(after Underwood, 1978).

For a larger animal to sustain itself on poorer foods it must travel more and expose itself to greater dangers in a less well-known range. This is the frontier on which the kudu stands, a frontier that has not been met by other tragelaphines and has been passed only by the eland. When home ranges are compared (p. 133) it can be seen that an eland needs a foraging area between four and ten times that used by a greater kudu. For larger ranges to be covered more easily and for an easy avoidance of danger, the eland's adoption of a sustained long-strided trot is a particularly effective and energy-saving gait. To achieve this the conventional tragelaphine proportions and musculature (which are better suited to walking and bounding) have had to be modified. Over-extended neck, head and horns, slender under-muscled legs have all had to become more compact. It is the



Foreleg and metacarpus in left: greater kudu; middle: Derby's eland; right: common eland.

combination of this need for compact musculature with greater size and an inheritance of male hierarchy in the social system that has helped transform the frame of an eland. In contests between male kudu, ritualized displays are backed up by horn wrestling, in which it is the qualities advertised in the display, that is height and horn-length, that provide leverage and tend to determine the issue. Weight is less important because a tall narrow body



Lateral display of head and shoulders in left: greater kudu; middle: Derby's eland; right: common eland.

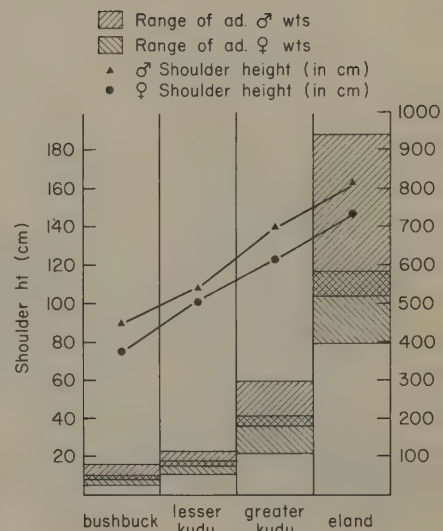
is generally unstable. In the eland a lowered centre of gravity, shorter limbs and neck and a more muscular body change the test into one of relative weight and strength. To cope with the extra stresses put upon horns during wrestling they have had to become very much stouter and, to the spiral's function of providing "engagement" surfaces must be added the need for reinforcement in the main shaft.

Competition between male elands favours weight more than any other factor: as a result bulls continue to put on weight almost throughout their lives. The gross disproportion in a male eland's dimorphism can be graphically illustrated in a comparison of weights in both sexes of bushbuck, lesser and greater kudu and eland with their shoulder-heights which follow a less eccentric gradient.

Further implications are discussed in the profile of Derby's eland which is in many respects intermediate between the eland and the kudu.

When the living tragelaphines are viewed as an evolutionary array they provide particularly apt illustrations of the roles of climate, habitat, food distribution, body size, limb proportion and social system in determining the peculiarity of a species. Further study will allow us to appreciate further the adaptive character of their subtly different shapes and behaviour.

The strong family resemblances in this group are matched by an unusual readiness to hybridize in captivity. The following crosses have been recorded: eland and kudu, lesser kudu male and sitatunga female, lesser kudu male and bushbuck female, bushbuck and sitatunga, bongo male and sitatunga female.





Sitatunga
(Tragelaphus
spekei)

Family

Bovidae

Order

Artiodactyla

Local names

Nzohe (Kiswahili), Nzobe (Runyankole),
Njobe (Lutoro, Lukonjo), Ngabe
(Luganda), Lebadzi (Madi), Isune
(Luhya), Dwe (Lwo), Emalit (Ateso),
Ntambantamba, Katukutu (Kifipa).

Measurements

head and body

152—170 cm males

135—155 cm females

height

100 (88—125) cm males

(75—90) cm females

tail

20—25 cm

weight

100 (79—125) kg males

(50—57) kg females

horns

66 (45—90) cm

Sitatunga (*Tragelaphus spekei*)

Races

Tragelaphus spekei spekei Uganda, north-western Tanzania, West Kenya
Tragelaphus spekei selousi Tanzania

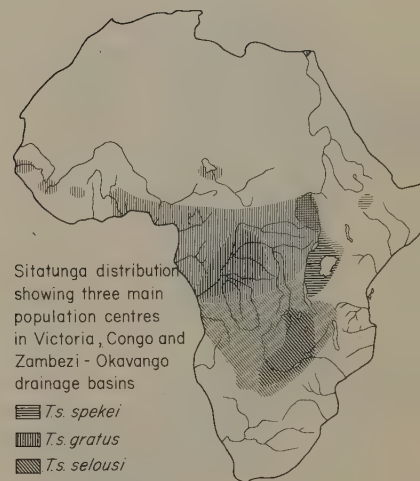
The sitatunga is a large shaggy antelope distinguished by its long splayed hooves, which are adapted to walking in thickly vegetated and muddy swamps and marshes. Not only are the hooves splayed but the entire stance of the animal tends to be rather pyramidal when moving over boggy ground.

The sexes differ in size, build and colouring. The males are larger and bear rather heavy, sharply keeled horns that describe a shallow spiral with one and a half twists. The male *T. s. spekei* is grey-brown on its upper parts without stripes or with only a suggestion of them and the dorsal crest is often dark. The female is rufous with eight or ten distinct white stripes. However, the occasional individual is coloured rather like the male and Meinertzen (1916) suggested that such colouring might be associated with old age as he never saw a brown female with young. A hybrid sitatunga-bushbuck male that was castrated at the age of five was observed to change its colouring from dark brown back to the reddish colouring of adolescence, which implies a hormonal control in both sexes. The male of *T. spekei selousi* is yellowish to dark brown with faint stripes and spots. The females of this race vary from bright chestnut to light or dark brown.

The overall distribution of subspecies suggests that there are three populations, each centred on a river system or drainage basin. The largest basin is that of the Congo (Zaire) River and the race occupying this region, *T. s. gratus*, has the most extensive range. Sitatungas from as far afield as Gambia and Lake Chad have been allocated to this subspecies. Like most of the other tragelaphines, *T. s. gratus* is strongly striped and patterned in both sexes, which could indicate conservatism or that predominantly forested swamps favour the retention of strong patterning more than the exposed reedy habitats further south and east.

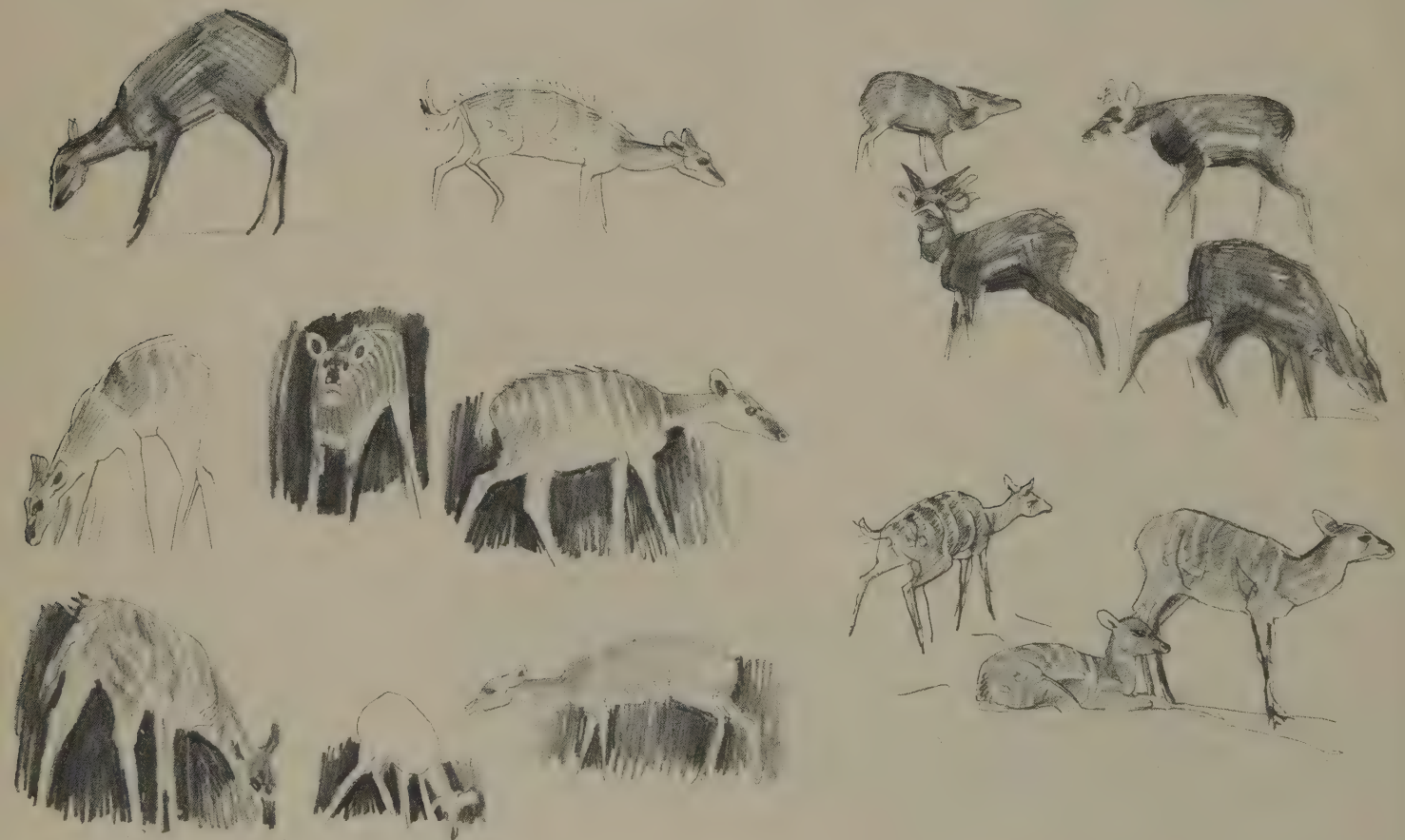
The eastern population, *T. s. spekei*, centres on the Lake Victoria basin while the range of the southern sitatunga, *T. spekei selousi*, encompasses the Bangwelu, Zambesi and Okavango basins. The sitatunga of the Nile Sudd, *T. s. larkeni*, is strongly patterned and Mackenzie (1954) synonymized it with *T. s. gratus*.

This highly specialized antelope is closely related to the nyala, *T. angasi*, which shows no sign of adaptation to marsh living and inhabits the south-east corner of Africa. Although it is conceivable *T. angasi* has made a secondary return to *terra firma* it is also possible that *T. angasi* is a direct descendant from, or the relic of, a common ancestor. They are in any event almost impossible to tell apart on the basis of bones. Fragmentary fossil horn cores and teeth that have been allocated to *Tragelaphus spekei/angasi*



come from a variety of east and south African Plio-Pleistocene sites and are the earliest tragelaphine fossils known. Of course these fragments tell nothing about the age of the sitatunga's adaptation to marsh living but it is possible that the species is a modified relic of a stock that is close to the ancestry of all other living tragelaphines. The species' invasion of swampy ground is most likely to have started within the forest and only when the ecological transformation was complete is it likely that the species emerged from swamp forest into reed and papyrus beds.

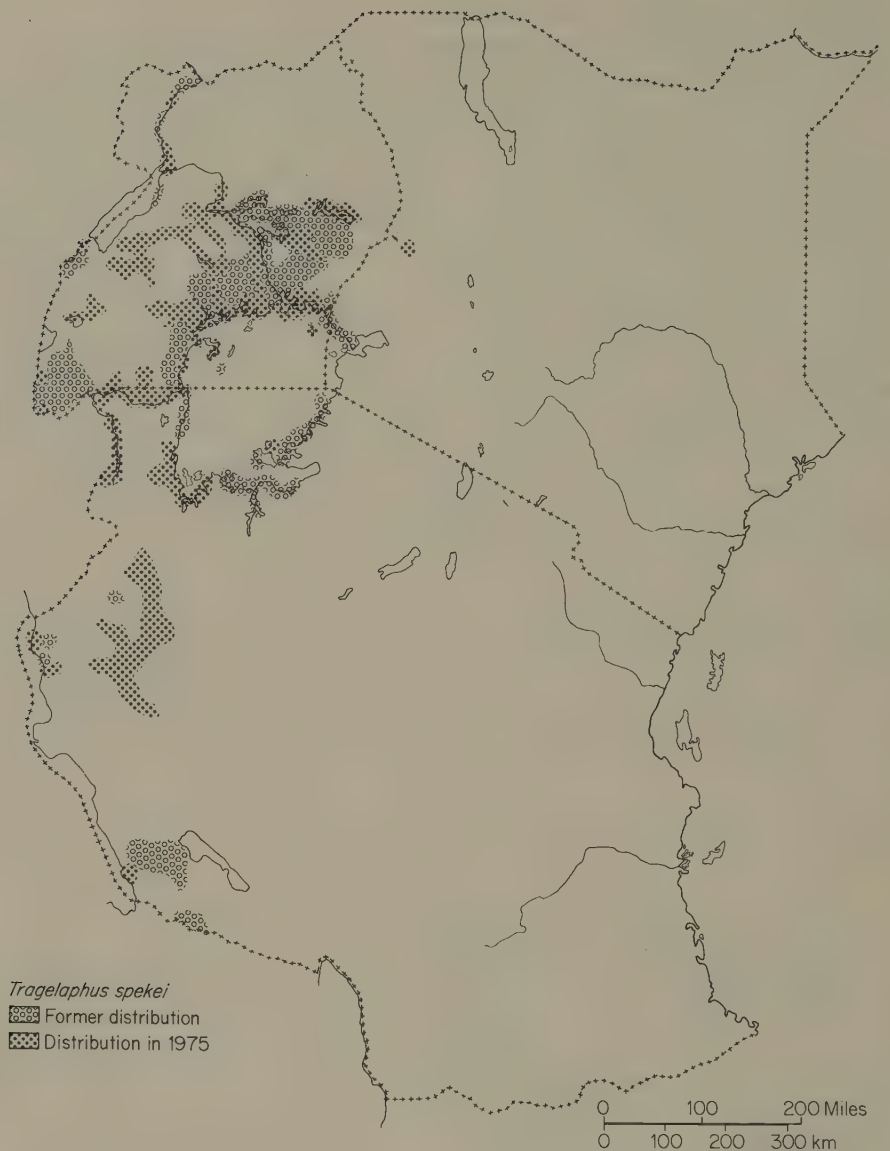
That the length of the hooves can be slightly modified has been demonstrated by the sitatunga living on the isolated Nkosi Island in Lake Victoria. This rocky island is about 80 hectares in extent and although forested has no boggy ground or marsh. In 1915 Meinertzhagen collected specimens of Nkosi sitatunga and quite unjustifiably erected a new race, *T. spekei sylvestris*, on the strength of slightly shorter hooves. In any case it was quite unrealistic to give this herd (which may have been exterminated by now) an equal status with subspecies ranging over many thousands of kilometres. At the time the island was mapped in 1900 the local people stated that there were ten to thirteen sitatunga on the island. By the time Pitman visited this island in 1927 he estimated the numbers to have grown to at least 150 and likened the island to a cattle pen. Considering their inbred nature the Nkosi sitatunga's peculiarities might almost be likened to those of a select thoroughbred herd, except that one can have no idea of the age and length of its pedigree.



Wherever possible sitatunga like to browse off the leaves of bushes, thicket and other low-level vegetation growing along the margins of marshes, rivers and lakes. Hale Carpenter (1925) described them browsing very heavily off the Annonaceae on Bugalla Island, which are *Monodora myristica*, *Uvaria bukobensis* and *Xylopia aethiopica*. In Saiwa, western Kenya, Owen (1970) showed that the number of animals was higher in those sections of the swamp that were next to riverine forest. Around Lake Victoria, *Alchornea* is a favourite browse and at Saiwa the leaves of *Oenanthe palustris* and *Hydrocotyle ranunculoides* were amongst the most commonly eaten foods. Owen also recorded them eating *Desmodium repandum* and *Phyllanthus capillaris* in the forest strips. Like other tragelaphines they eat fallen fruit and chew the bark of some trees and bushes. However, over very large areas of its range the sitatunga is almost entirely dependent on vegetation that is not woody and individuals may even emerge from their retreats to graze on new grass. A most important food in most swamp areas is the bullrush, *Typha*, and Owen (1970) recorded the flowering spikes of *Echinochloa*, *Miscanthidium*, *Pennisetum haareri*, *Pycnus lanceus*, the young shoot tips of *Polygonum* species, together with *Hygrophila spiciformis*, *Hydrocotyle ranunculoides* and *Ranunculus multifidus* as the most commonly observed foods in Saiwa. In the Bangwelu swamps, Manning (personal communication) found them feeding almost exclusively on swamp grasses and sedges such as *Cyperus digitatus*, remaining on the same spot for long periods and moving rather little and very slowly. In forest they will even rise on their hindlegs to reach leaves and I have seen a male use his horns to break a branch, which he subsequently nibbled. In swamps they will feed standing in various depths of water or supported on mats of floating vegetation but they will immerse all but their eyes and nose for long periods.

The coat is greasy and a film of oil tends to float off on immersion in water. They are good, but slow, swimmers and have been found lying up in water out of their depth. Nonetheless, they often rest on dry mounds or termitaries in the swamp or in places where there are many dense tussocks of tall reeds. In these spots they turn round to trample themselves a springy mat to lie on. This trampling and turning is a characteristic of the species even in captivity. The action compresses vegetation and helps make a dry bed in an otherwise water-logged environment. This is particularly important for the young, which are generally found lying up on well-hidden platforms. Continual trampling also maintains pathways, which because of the height of the surrounding reeds and papyrus give the appearance of tunnels. Some of these are used regularly by several animals, others are temporary. Animals often feed very intensively in a small area for some days or even weeks and then desert it. Browsing is seldom an aimless wandering, but tends to be an activity that is spatially and temporally restricted. They are mostly inactive from about 10 or 11 a.m. to about 5–5.30 p.m., then they walk to their current feeding ground until between 8.30–10.30 p.m. This evening feed is probably followed by a long rumination period and feeding is resumed before dawn and often continued until late morning if the animals are not disturbed. However Manning (personal communication) has seen them grazing out in the open in the middle of a hot day in the Bangwelu swamps.





The fact that there is a rich year-long supply of greenery in their habitat allows exceptionally small home ranges and a potentially high density. For instance, Owen (1970) never saw an individual beyond 500 m of another and estimated about seven animals per linear kilometre of riverine swamp. Manning has also found individuals restricting their activity to a fairly small area and the same animals were seen in very much the same places over a period of two years. Numerous hunters have also affirmed the attachment that individuals have for a small area. Nonetheless, they are occasionally seen emerging from their normal haunts and males seem to be more mobile than females in this respect. There have been interesting observations of social groupings which may be correlated with high densities. For instance, on Bugalla Island, Meinertzhagen (1916) saw twelve males, nine females and five juveniles simultaneously within sight of a single territory, likewise,

Bostock (1946) saw 19 animals at one time in Ipeta swamp but they were clumped in twos and threes and these groups were not likely to have been within sight of one another. They comprised adult pairs or females with or without immature animals. In Bangwelu, animals are essentially solitary but Manning saw temporary aggregations of up to seven gathered for a few hours on dry pastures within the swamp. Owen (1970) never saw an adult male in close proximity to another, and larger groups, numbering up to nine, were never accompanied by more than one adult male. She never saw a fight and males probably avoid one another. In contrast, adult females are frequently but impermanently sociable. That their gregariousness is not influenced by males was shown by Owen's sighting 68 groups containing two or more adult females of which only 16 included an adult male. Nor are these nursery herds, for only 27 of Owen's groups contained immature or juvenile sitatunga. Because ranges are small, close neighbours are very likely to come together but there is no evidence of any permanence in their associations.

Like many other antelopes the young lie up for several weeks after birth but they might also remain more independent of their mothers than most antelopes. Meinertzhagen (1916) noted young ones on the Ssesse Islands resting on their own in the open and Owen recorded 54 immature animals on their own and 33 in twos and threes that were unaccompanied by adults.

She recorded a squeaking contact call between sitatungas feeding and, like other naturalists, she was impressed by the crescendo of extraordinary barks uttered by the males, a sound which is most often heard at night and may be answered by other males. This sound is frequently associated with movement, being uttered both by males faced by an unidentified disturbance in their immediate vicinity and by males running off through the reeds. Meinertzhagen heard a male that had taken several tumbles while trying to run down a hillside on its clumsy feet keep up barking for nearly half an hour, and at night it is not unusual to hear an individual bark for many minutes on end. Barking is probably one of the most important ways in which the males advertise their presence and so may help to avoid direct confrontations. Females also bark but less frequently and it is generally a single short sound more like a loud sneeze, apparently uttered in alarm. Fights have been seen only in captivity, both contestants lower their forequarters and splay out their legs. They have been described fighting vigorously with forward and upward thrusts and butts from their low stance.

Like bushbuck, sitatunga are much bothered by flies, which are perhaps attracted by their oily secretions. These and the inguinal glands may also play an important part in communicating information about the sex and status of individuals and further assist mutual avoidance between males.

Their gait is very clumsy, particularly on broken terrain, but they are normally quiet and deliberate in their movements and only bound in great floundering leaps when excited or forced to break cover by a very close approach. Otherwise they avoid attention by cautiously entering thick vegetation, where they keep quite still, or by sinking down into water very slowly, leaving only the snout or part of the head above the surface.

Their most important natural predator is likely to be the python, although they might have been severely restricted by crocodiles when these reptiles



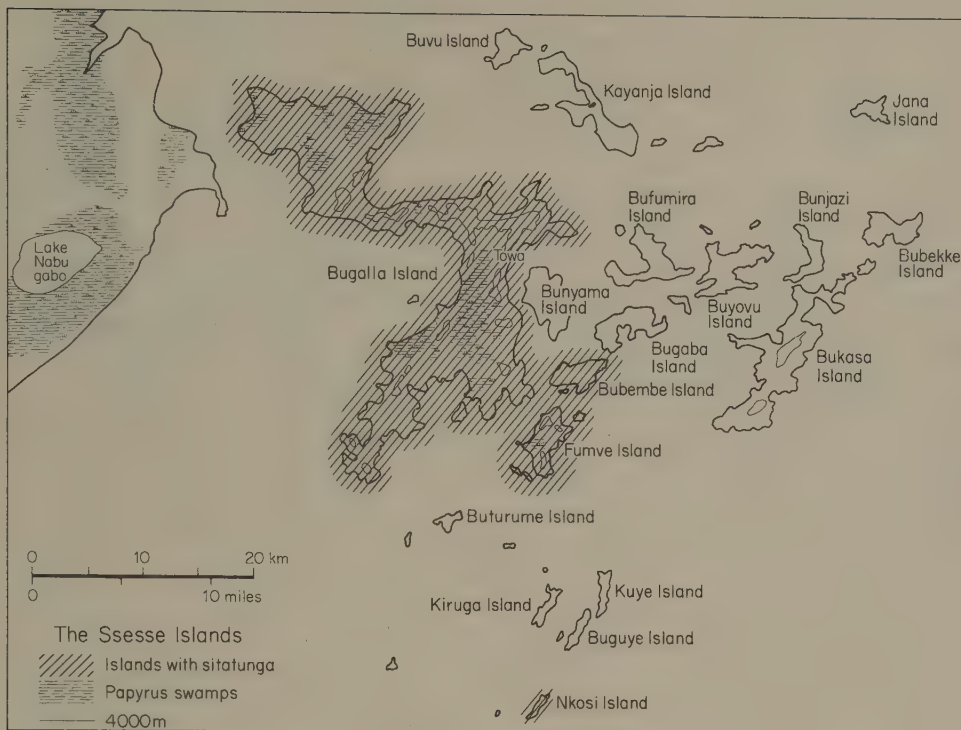


were numerous. Sitatunga have been recorded killed by lions and wild dogs. They are probably attacked by leopards in some areas and their young taken by serval cats, jackals, crowned hawk eagles and, Pitman (1928) suggested, even by otters. Because of their regular use of paths and tunnels, sitatunga are particularly vulnerable to persistent snaring with simple wire nooses in swamps that are close to human settlement. Communal hunts for sitatunga are popular in parts of Uganda. Hundreds of men and dogs beat through the marsh. Sometimes the animals are driven into long lines of hemp and sisal nets, or the papyrus is fired, and in some areas hunters also take to canoes to get animals in deeper water. Notwithstanding their effect, these community hunts probably have a less depressing effect on sitatunga numbers than snaring, as the group effort is only worthwhile in places where the animals are numerous. In Bangwelo, Manning (personal communication) has found sitatunga quite tolerant of human settlement so long as its cover is not removed and he remarked that control of fire in the swamps is essential to any conservation effort. The meat of the sitatunga is generally appreciated, hides serve as mats, and the horns were widely used as musical instruments in the past. In Madi, these horns used to be worn on the head in traditional ceremonies.

Human history appears to have had a rather interesting effect on sitatunga in the Ssesse Islands in Lake Victoria. In common with other parts of Uganda these islands were devastated by the arrival of human and bovine trypanosomiasis at about the turn of the century. Large herds of cattle and about 20,000 people lived on the Sseses at the end of the nineteenth century, yet by 1909 the cattle were finished and the remaining people had to be evacuated leaving the island to the tse-tse flies and to a process of natural regeneration that was unaffected by man until 1920, when the trypanosomiasis came under control and a trickle of islanders started to return. Before the sleeping sickness arrived, there had been so many people on some of the islands that they were forced to use tied grass bundles for fuel because wood was so scarce (Thomas, 1941). On such islands it is inconceivable that sitatunga should have survived and it is interesting that in spite of their ability to swim and the massive regeneration of suitable habitat all over the Sseses, many of the islands were not recolonized by sitatunga, although they became a dominant feature of the fauna on two large islands and a number of smaller ones. By 1915 sitatunga were very numerous on Bugalla and Nkosi islands (Meinertzhagen, 1916). By 1925 Hale Carpenter described the undergrowth on Bugalla Island as having been destroyed by the sitatunga and the animals were also extremely plentiful on Bubembe, Fumve and Nkosi islands; yet they were still absent from Bubekke, Bukasa, Bunjazi, Bunyama, Mbugwe, Kuye, Buguye and Kiruga.

It is known that a few sitatunga were present on Nkosi at the turn of the century and that the ancient Towa forest and some papyrus swamps may have harboured them on Bugalla. The nucleus for the Fumve Island population had probably found its refuge in a very large papyrus swamp. The moist climate of the Ssesse islands encourages a rich growth of annuals and the removal of man and his domestic stock was immediately followed by woody growth at the right height for ungulate browsing.

Sitatunga. a. Uganda mainland; b. Nkosi; c. Bugalla.



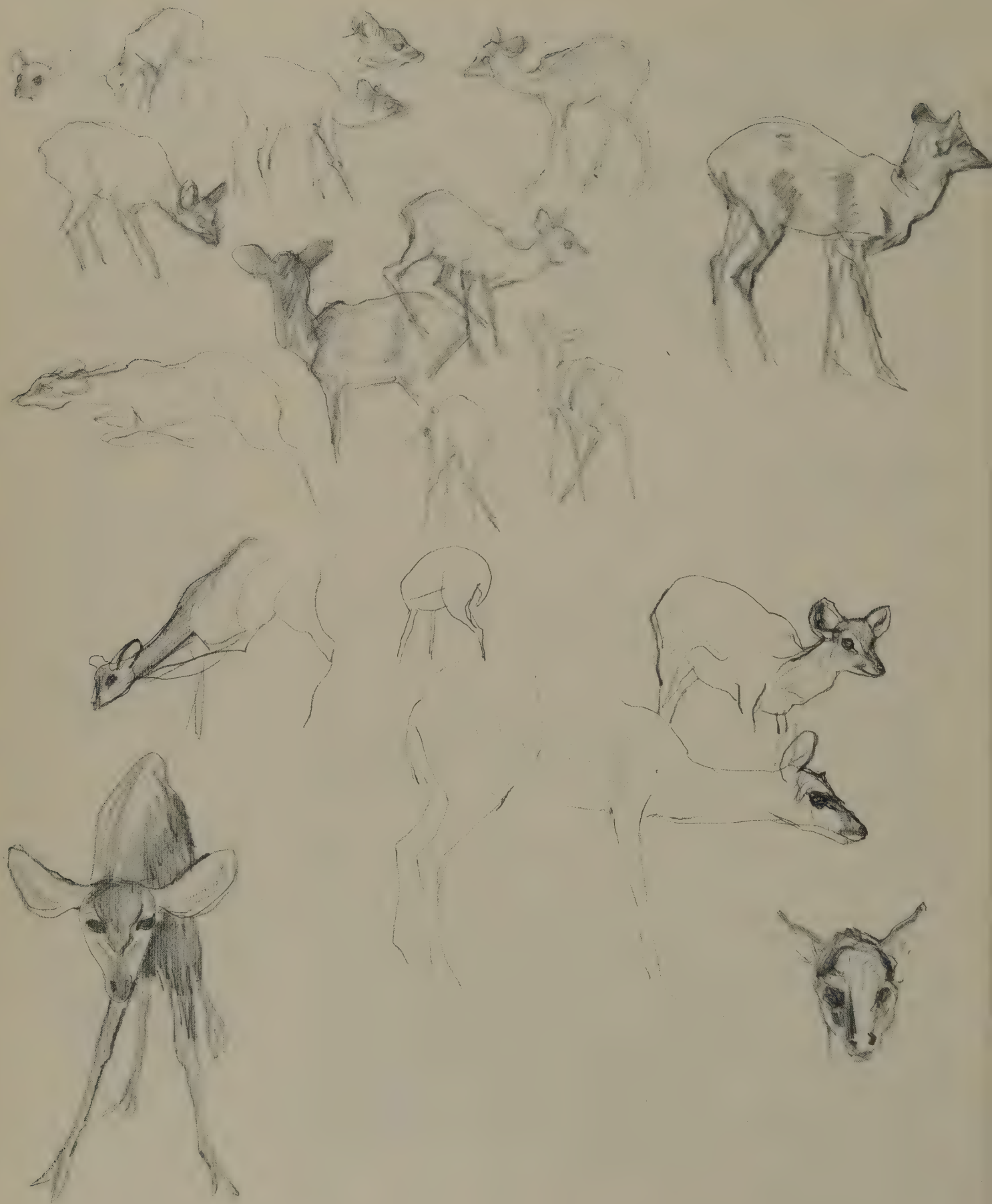
In the absence of predators the animals became extraordinarily tame and in 1915 Meinertzhagen was actually able to stroke them as they walked past. Ten years later, Pitman visited Nkosi island and wrote:

“these animals are today in no whit more shy, time and again individuals stood and looked at me from a distance of a few feet. In several instances hand-clapping and shouting produced no effect and I saw one of the beaters hit one buck several times with a stick before he could turn it and drive it in front of him. This exhibition of boldness was almost wholly confined to the males and the females were noticeably shyer.”

In 1928 Pitman remarked on the sitatunga grazing at all hours of the day and their fearlessness when feeding: he never saw one attempt to take to the water.

In the absence of predators and competitors it is scarcely surprising that the sitatunga multiplied enormously in the Sseses but their ability to colonize other islands or swamps that are not contiguous is presumably inhibited by extremely sedentary habits. Crocodiles might also have diminished the chances of their surviving a swim across open water and the original colonization of islands in Lake Victoria is likely to have been assisted by the very large floating islands of papyrus that are blown about the surface of the lake from time to time, bearing entire communities of animals and plants with them.

Single males have been seen to emerge from the swamps and wander more widely during the rains in several localities on mainland Uganda and



Tanzania. Nonetheless, the extent of wandering may not be very great and the trait appears to be restricted by season and also to males, in which case it would be unlikely to assist the dispersal of breeding populations. In Bangwelo, Manning observed an increase in the size of the overlapping home ranges during the flood period, provided food and cover were available. This applied to both sexes. It would be interesting to know more about the seasonal dispersal of sitatunga, because, when Pitman visited Nkosi Island in April 1928, he thought that the sexes were partially segregated, with the females tending to concentrate at the northern end of the island where the cover was thicker. The rains are at their height in April and the majority of births appear to take place at that time in south-western Uganda. Owen (1970) has also found peak rainfall and births co-inciding at Saiwa but it was evident that breeding was continuous in western Kenya and any general social pattern was likely to be obscured by this and by the absence of marked seasonal changes.

Since the gestation period lasts about seven-and-a-half months, there would be a tendency for the mating peak to take place in the dry season, when the animals have been naturally concentrated by drainage and loss of cover around the peripheries of their habitat. It is in this respect that the Bangwelo pattern appears to accord with that of East Africa, for Manning has observed that mating must peak at the end of the dry season to produce a birth peak in July.

Males are slow but persistent in their pursuit of females. The latter, on the other hand, have been seen by Owen to depart from their usual caution and silence, moving away from the male in erratic bounds through the rushes and causing a good deal of disturbance, standing still for a few minutes and then dashing through another clump of vegetation. Like other tragelaphines, the male walks after the female with his horns flat on his neck: he rubs his cheek against her sides and rump and may push her neck down beneath his before mounting.

The young one is born on a trampled resting platform in the reeds, or in a "form" amongst thick vegetation and is then left on its own except for quick visits for suckling. Lying-up continues for several weeks but even after it begins to be mobile, the young is rather independent of its mother and ties are not strong. Half-grown animals sometimes lead a partly solitary life, feeding and resting on their own but Manning (personal communication) has remarked on their playfulness.

The male's horns sprout at about three or four months. Full maturity is reached at about four years and captives have lived 17 to 20 years.



Bushbuck
(Tragelaphus
scriptus)

Family

Bovidae

Order

Artiodactyla

Local names

Mbawala, Pongo (Kiswahili), Engabi (Luganda and many other languages), Leba (Lugbara), Boynet (Kipsigi and Sebei), Kulungucha (Kiliangulu), Imbabala (Nnyiha), Imbarwara (Kinyakyusa), Matu (Kihehe), Kungu (Kiamu), Aderit (Ateso), Ekoloba (Karamojong), Ruda (Lwo), Ol-bua (Masai), Welit (Kidorobo), Dol (Somali).

Measurements
head and body

117—145 cm males

114—132 cm females

height

64—96 cm males

61—80 cm females

tail

19—24 cm

weight

30—77 kg males

24—42 kg females

horns

26—57 cm

Bushbuck

(*Tragelaphus scriptus*)

Bushbuck are amongst the most vividly coloured and patterned of mammals; yet they are also subject to such a great deal of individual and regional variation that many races have been described. (Allen in 1939 listed 27 subspecies.)

All types and both sexes carry geometrically-shaped white flashes on the most mobile parts of the body, ears, chin, tail, legs and neck but males have darker areas, banked up against the white areas, which tend to be brighter and clearer. The effect is to increase conspicuousness of the slightest movement and to emphasize the conformation of any posture that the male adopts. Most particularly these markings enhance the male's displays.

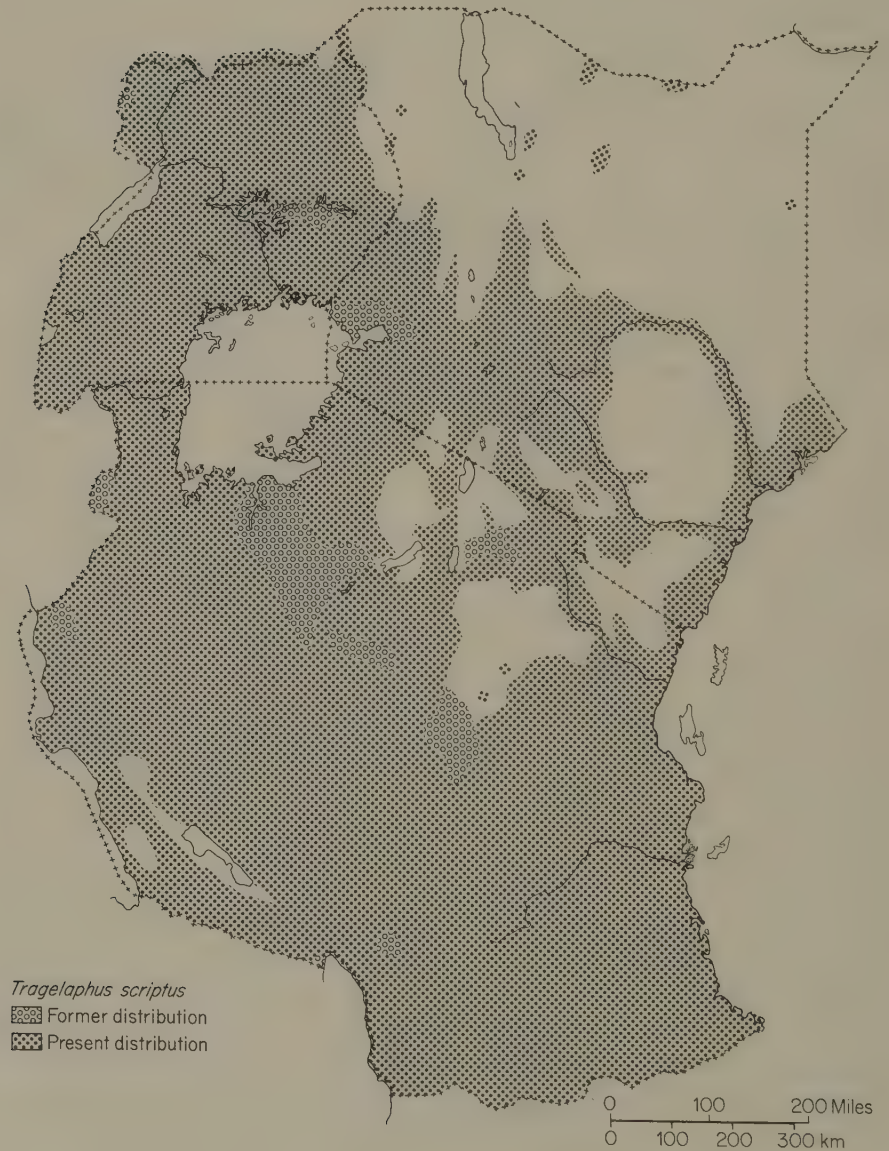
The strongest contrasts on the extremities of the body are to be found on males from forest-dwelling populations, while weaker contrasts are seen in animals living in drier, more open habitats. There are possibly two distinct factors responsible for this trend: one is the general tendency for populations in humid environments to be darker and often redder (Gloger's rule), while animals from arid areas are generally lighter and more yellowish. The other factor might concern differing selective values for advertisement in the more open and closed habitats. Bushbuck are slow and are easily caught by predators in the open. They rely on freezing for escape, or a short dash into thick vegetation, so that the social advantages of bold patterning are perhaps tempered by increased vulnerability in more exposed habitats.

Turning from the extremities of the animal to the body itself, it is clear that the pattern of dorsal stripes is also strongest in bushbuck populations from the main African forest block ("harnessed" type) and is weakest in the "sylvan" bushbuck from the southern and eastern half of the continent. It is possible that stripes originated from juvenile camouflage and that their elaboration in tragelaphine adults is connected with socio-sexual behaviour (see pp. 38, 72). It is interesting, therefore, that a genetic trait should have arisen, probably through isolation in a more open habitat, in which this feature was suppressed in both sexes. The ready interbreeding of the two forms shows that the possession or absence of stripes does not affect sexual behaviour but there must be something about the forest habitat that is linked with the persistence of stripes. I have suggested earlier (p. 72) that bonding may be more important in forest habitats. It would therefore be interesting to compare the details of courtship and other social behaviour in bushbuck from purely "harnessed" and "sylvan" stocks.

Bushbuck living in the high mountains of eastern Africa are often larger, darker and hairier than those living in the surrounding lowland and some have been described as distinct races (i.e. *T. s. barkeri* from the Imatong and Karamoja Mountains, *T. s. heterochrous* from Mt Elgon).

Practically every extreme in pattern and colouring can be found in eastern Africa. This is because this area is the principal area of overlap between the "harnessed" *scriptus* and the "sylvan" *sylvaticus* types. Intermediate

forms are found throughout the cross-hatched area on the map (p. 98); possibly they represent the result of long-term hybridization. The shaded area on this map indicates areas where, in addition to intermediates, animals that are representative of both extremes can also be found, with the harnessed types mostly in gallery or relic forests and sylvan forms in the savannas.



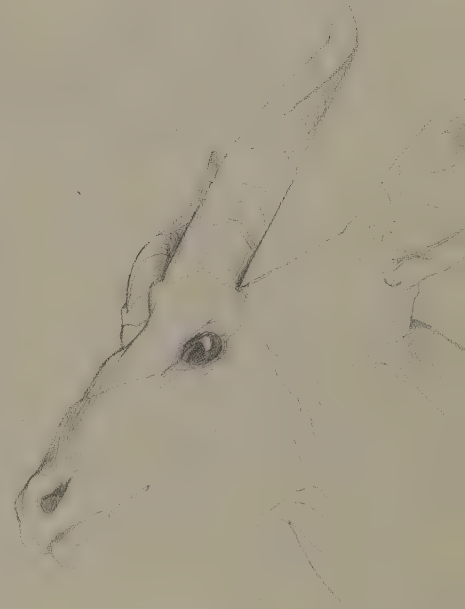
When I was examining nearly 1,000 bushbuck skins collected by the Tse-tse Control Division in parts of Acholi and Bunyoro I found patterns ranging from a complete harness (as illustrated on p. 98) to unmarked ones like Fig. M. Unfortunately this selection was accidentally dispersed and the opportunity to illustrate the full range of variation possible in one locality was lost. However, the colour plate facing p. 98 shows the broader geographic trend and also illustrates the principal types of variation in bushbuck. These are: (a) geographic, (b) sexual (compare B and C.), (c) climatic (compare J. and L.), (d) individual variation (compare striped offspring of K. with almost plain mother). Figures E., F. and G. show three males from the same locality. The influence of age on colouring has not been shown but many males get progressively darker as they get older. However, this is not invariable; for instance, the light male D. was an old animal. This factor is probably controlled by testosterone, because castration is known to change coat colour considerably and to halt all horn growth. Other male characteristics that are highly variable are the shape of the horns, the colour of the dorsal crest and the conformation and colouring of the neck. The development of all these features may be controlled by hormones and this point is discussed further in relation to social behaviour.

The ecological range of the bushbuck is extraordinarily extensive but the species is essentially dependent on thick cover, even if this is no more than small thickets centering on termitaries. They need some water but can subsist on dew. They range up to 3,000 m on East African mountains and they sometimes live in reedbeds. That they are especially numerous in some forests but not in others is probably determined by the state of the undergrowth, which must serve both as cover and food.

Foods vary with the habitat but shrubs and leguminous herbs provide a large part of their diet everywhere. The locally dominant trees and shrubs often provide browse; thus *Combretum* leaves are commonly eaten in the moister savannas, *Capparis*, *Strychnos*, *Abutilon*, *Dalbergia* and *Grewia* in thickets and *Maesopsis* and *Albizia* saplings along forest edges. Growing grass may be important for populations living on the edge of open country. The pods of *Acacia* spp. and other fallen fruit are favoured foods and the fruits of *Ficus*, *Ricinodendron*, *Cordia* spp. *Balanites*, *Diospyros*, *Parinari*, *Sclerocarya*, *Ziziphus* and *Dichrostachys* are among those recorded. Wilson and Child (1964) gave lists of foods eaten by bushbuck in Zambia according to month and they noted that most foods were seasonal but that grass was eaten throughout the year. Bushbuck have also been recorded eating the fallen flowers of *Spathodea*, *Kigelia* and those of *Dolichos* and *Tecomaria*. Kolbe (1948) noted that they are especially fond of a marsh-growing *Convolvulus*. They are selective and dainty feeders and move quietly, pausing frequently while foraging.

In many areas bushbuck are crepuscular or nocturnal animals and there is minimal activity wherever they are likely to be harassed during the day, but diurnal feeding and movement can be seen in many undisturbed habitats and during cooler seasons.

Bushbuck invariably choose to rest on their own and are therefore most frequently seen as solitary animals during the day and they sometimes sun





A A dark morph of "*scriptus*" type: male

B Typical "*scriptus*" type: male

C Typical "*scriptus*" type: female

D A light morph of "*scriptus*" type: male

E } Three males from a single locality
F } (Kasulu, Tanzania) to show variation
G } in pattern and colour

H Pale male from Ujiji Tanzania

I Ethiopian Mts "*decula*" type: male

J Pale type from Moyale, North Kenya
"*meneliki*" type: male

K }
(K2) } Four animals from a single high
altitude locality (Mt. Elgon)
L } (K + K2 : female)

M }
N Male from Fort Portal Uganda

BUSHBUCK



harnessed (*scriptus*) types



plainer (*sylvaticus*) types



area of overlap and / or intermediate types



Zone of maximum variability plus co-existence of both types

- 1 *T. scriptus scriptus*
- 2 *T. scriptus sylvaticus*
- 3 *T. scriptus roualeyni*
- 4 *T. scriptus ornatus*
- 5 *T. scriptus bar*
- 6 *T. scriptus delamerei*
- 7 *T. scriptus meneliki*
- 8 *T. scriptus decula*

The numbers broadly correspond with the nomenclature followed by Ansell (1968).



Plate shows A-N "*scriptus*" types (predominantly Western Forests) and "*sylvaticus*" J, L, M types (predominantly Eastern) with many morphs in overlap area + horn variation.

B-C, K-L: Sexual variation; J-I-L, A-D: Climatic variation; E-F-G-H and K-(K2): Individual variation.



themselves in the early morning. This desire for seclusion when resting is also very marked in captive animals, and at least half an animal's time is spent on its own. In the Nairobi National Park, Allsop (1971) found that bushbuck did most of their feeding at night, preferring dark and cloudy skies; most of their activity centred on the bush-grassland margins, where there is a rich variety of herbs and grasses. Tame, free-ranging animals tend to feed, ruminate and rest at irregular intervals throughout the day and night. Waser (1975a) found that bushbuck in the Ruwenzori National Park "distributed their activities in a pattern of short-term cycles" and that nocturnal grazing was common in July.

Individuals often react in surprisingly different ways when they are encountered on their own. In thick bush or forest they may sink to the ground and lie still and flat or they may bound away, making a series of hoarse barks. If lying in an exposed spot they may leave rapidly and generally silently, or they may sit on quietly. Even when standing in the open they may stand still or slowly stalk over to the nearest bush. Their run is slow and clumsy, except that in thick bush they are adept at disappearing. This is due to their using well known, but not necessarily conspicuous, paths and to freezing, often no more than 50 m away from where they started. Verheyen (1951) noted that young males tend to raise their heads in alarm, whereas older males lower their heads. The functions of barking in tragelaphines have been discussed earlier and it is interesting that Jacobsen (1974) saw a female bark in circumstances similar to mobbing:

"The female, once she had spotted the predator came running out of the long grass, barking, her eyes fixed on the leopard. When the latter moved on she made one bound in its direction, stopped and barked and repeated this performance several times until the leopard had passed from view. The latter then passed the hiding place of two adult bushbuck, who leaped out, barking and ran off in opposite directions, but away from the predator."

Any disturbance may precipitate this call and the same author has described several animals running about aimlessly and barking when a thunderstorm was approaching. Kolbe (1948) suggested that when barks are uttered in series they indicate the direction of movement. The timbre of the voice is less raucous when females or young bark.

The role of scent in the life of the bushbuck is difficult to assess. Both adults and subadults have active inguinal glands that produce a secretion and animals have been seen to track one another by scent alone. The ears, crown, cheeks and neck are often scented and oily and these sites are the principal areas mutually licked by these animals as well as being rubbed on branches and other vegetation. Jacobsen (1974) has interpreted the latter habit as evidence of territoriality but it is more likely to be an incidental scenting of the home range. Sometimes these secretions seem to be the source of considerable irritation, as flies are particularly attracted to these areas, and a bushbuck on the forest edge will often shake its head and race off to cover in what appears to be a deliberate effort to evade flies.

Their vision is sharp and they are quickly alerted to large carnivores in the open. Notwithstanding this, sight may be relatively unimportant within a secure, well-known habitat. For example, a pregnant female was



killed in the high-altitude forest on Mt Elgon that was completely blind in both eyes and yet in excellent condition in spite of its disability.

Bushbuck are capable of living at very high densities and estimates run as high as 26 per sq. km (Waser, 1975a) in a well-bushed corner of the Mweya Peninsula. Tse-tse extermination campaigns have also bagged relatively large numbers; for example, 14,256 bushbuck were shot in 3,100 sq. km of Ankole and Masaka. This gives an average of 4.6 per sq. km for an area with very extensive grasslands and other habitats only marginally used by bushbuck, so that the actual density must be very much higher, particularly if one remembers that the population had not been eliminated in the end.

Individual ranges overlap very extensively, Allsop (1971) has estimated them to cover 0.25 ha to 2 ha in the Nairobi National Park while Jacobsen estimated ranges of 6 or more ha in a drier Rhodesian habitat.

Except for the mother and her young, associations are very temporary and the species is fundamentally solitary. Although contacts are frequent small ranges and solitary habits ensure that only a limited number of potential companions are available and the majority of these are probably fairly closely related.

Samples of bushbuck home ranges in Nairobi National Park (after Allsopp, 1971).

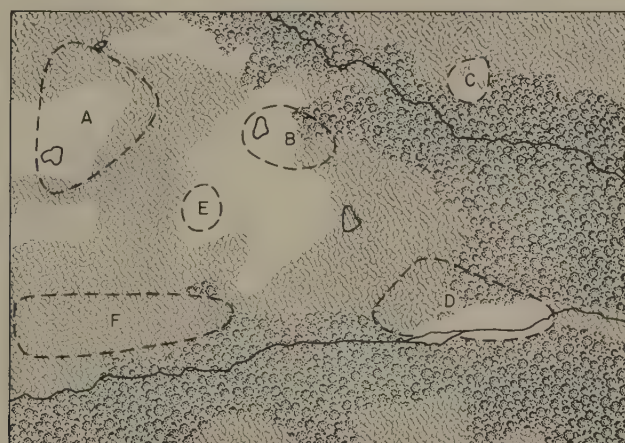
Group A: 4 adult males, 5 adult females, 3 subadult males, 3 young.

Group B: 1 adult male, 4 adult females, 2 subadults, 2 young.

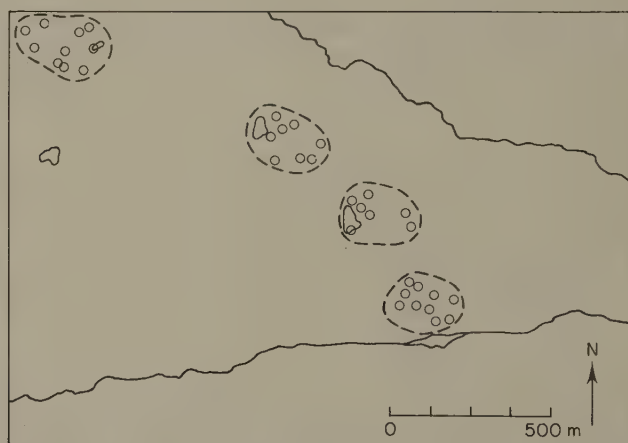
Group C: 1 adult male, 1 adult female, 1 young.

Group D: 1 adult male, 6 adult females, 4 subadult males, 3 young.

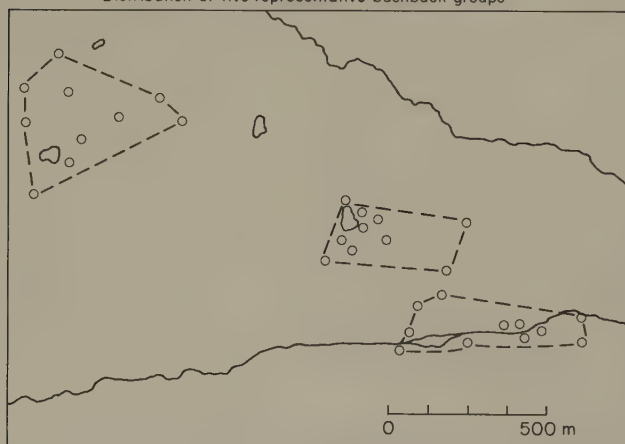
Group E: 1 adult male, 1 adult female, 1 young.



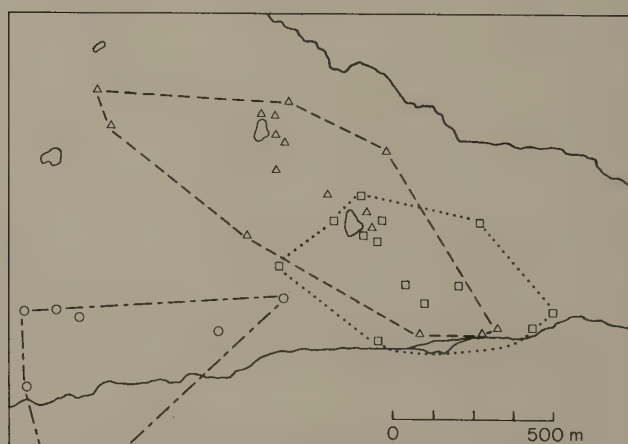
(a) = Bush = Forest = Grassland
Distribution of five representative bushbuck groups



(b) Home ranges of four female bushbuck



(c) Home ranges of three male bushbuck



(d) Home ranges of three sub-adult male bushbuck

In East Africa, many bushbuck habitats are discontinuous in that they are broken up by open areas, ravines and rivers, encouraging groups to live within naturally defined boundaries. Allsop (1971) mapped individual ranges in the Nairobi National Park and found that adult females had the smallest ranges (average 0.25 ha), subadult males ranged much more widely (up to 2 ha) but adult males tended to live in a more restricted area with age (average 0.56 ha). Up to six males and six females may share a large part of their home range but both Allsop and Jacobsen found that adult individuals have separate areas which they prefer and in which they commonly lie up. Away from these solitary refuges there may be loose associations that last for a few hours or a few days. The only animals that are commonly seen to avoid or threaten one another are mature males. Younger males are more sociable but even so they commonly horn bushes or ground, particularly in the vicinity of other males.

An age-based hierarchy is suggested by the tendency for older males to threaten younger ones, which will in turn threaten lesser males down the line (Jacobsen, 1974). Within a limited area fights and displays will become minimal once a stable order has been established and an unseen hierarchy probably underlies the normally tolerant behaviour of bushbuck communities. However, deaths, the incursion of immigrants, the maturation of younger males and perhaps the coming into oestrus of females would cause a disruption of the social order and it is in such circumstances that males would fight in earnest. Deaths and wounding have been reported but it is much commoner to see highly ritualized displays in which clashing of horns may or may not play a part.

In the course of a long dry season I once had the opportunity to observe increasing numbers of bushbuck gather along the foreshore of a small lake. Drought and a general absence of greenery had forced the animals off the surrounding hills where they were normally dispersed. On several occasions I saw displays and in one instance two well-matched males were watched by three other males and three females as they slowly circled one another with raised crests and tense high-stepping gait. Without any obvious signal the match came to a close with all nine animals dispersing in a centrifugal pattern. At higher intensities males leap into the air with arched backs and flaring crests and tail. The slow circling may turn to fast chasing interspersed with horn clashes.

When males do fight they may even charge from a short distance and engaging horns try to throw their opponent with powerful twists followed by stabbing. When this movement is not resisted the rival's horns may penetrate the throat, chest or side of the thorax. It is quite clear that fighting is potentially very disruptive and dangerous to bushbuck society and it may be this that has influenced the evolution of a most elaborate pattern and flamboyant display ritual, which is designed to impress and intimidate both females and rivals.

Because hierarchy is based on age, the bushbuck, in common with other tragelaphines, appears to have evolved a colour code to signify status, with the contrast of markings increased by a progressive darkening of the body colour with age, so that the older the male the more impressive he is likely to be. In this connection it is interesting that Morris and Hanks (1974) found





the oldest classes of bushbuck to be sexually active. The greater movement and range of a younger male might bring him into contact with more females and possibly with peripheral ones that would otherwise miss being inseminated. This eventuality seems to have been anticipated by an early sexual, as opposed to physical, maturity and Allsop found active sperm in the *vas deferens* of one-and-a-half year olds. The development of a crest, stronger contrasts of colouring and a thick neck possibly proceeds at a different pace in different individuals but nothing is known of the hormonal factors involved. A hand-reared male bushbuck in Uganda acquired these characteristics quite rapidly at the age of about two-and-a-half years and at the same time became slightly greasy at the base of the auricle (above the parotid and submaxillary glands). He also became aggressive and attacked his former keepers, a not unusual feature of imprinted antelopes. In the days before he was shot the animal flexed his neck, arched his back, displaying the newly grown crest, rolled his eyes and horned the ground and shrubs with great vigour as well as rubbing the sides of his neck and crown on branches. Other observers have stated that this intensely aggressive phase, or *ukali*, wears off after a few weeks but that an imprinted male cannot really be trusted after his first period of aggressiveness and that it recurs from time to time. The change in behaviour is probably due to a sudden rise in androgens, and other keepers have resolved the *ukali* problem by castration, which halts the development of all male characteristics and is followed by a return to pale red, female-type colouring.

Captives reared in isolation from other males do not necessarily develop at the same rate as free ones and possibly in the wild the presence of dominant males may influence the rate at which secondary sexual characteristics develop. If this were so, delayed development might provide a mechanism for accommodating a high density of males with the minimum of conflict and help the younger males to wander without precipitating fights.

A conspicuous feature of the behaviour of adult males is deliberate lying out near a termillary, tree trunk or other landmark but in a relatively exposed position. They are prone to take up position in the evening or early morning after a short bout of activity. Vesey-FitzGerald (personal communication) noticed males habitually choosing to sit with their backs against the edge of precipices in the Meru National Park, a site which, he pointed out, allowed them to be both relatively conspicuous but also to detect any approaching animal. It is possible that "lying-out" is a discrete compromise that allows the male's inguinal glands to scent the ground as well as to advertise the animal's presence to other bushbuck without rendering him vulnerable to predators. The male's attachment to a small locality has led various authors to describe bushbuck as territorial, however it is not an area that a bushbuck defends but rather a temporary association with an oestrous female.

Allsop (1971) described a fierce fight between two males which was witnessed by females. The contestants displayed in between fighting as they circled one another; the loser was chased off, after which the victor returned to the females.

As for other antelopes a female's urine provides the key to her condition. A squatting posture invariably excites an investigation by any male within

sight, after which he curls the lip. Males have been seen to track females by scent (Jacobsen, 1974) and it has been suggested that females instead are less sensitive to smell. Once a female is in oestrus she is very closely followed by one male and no other male is allowed near.

In courting, the dorsal crest is not erected and the head and neck are kept horizontal. A twittering call, specific to courtship, is uttered by the male while he follows the female, with cheeks and neck repeatedly rubbed against her flanks, he licks her vulva and eventually she stands still and allows him to mount.

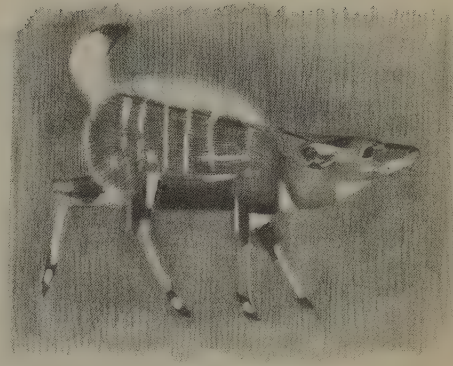
A calving interval as short as 166 days has been reported which implies a gestation period of no more than five-and-a-half months but Hamilton (1912) reported a seven month gestation. Other estimates lie between these extremes in the region of six months. Calving intervals of 225 and 334 days have been recorded in captives but a very short post-partum interval could allow biannual breeding. On the basis of 24 fetuses from south-central Kenya, Allsop estimated that there might be two birth peaks in this area, one in February, the other between July and September. Wilson and Child (1964) reported births in Zambia throughout the year but Morris and Hanks (1974) found evidence for a birth peak in this region at the beginning of the rains, October--November.

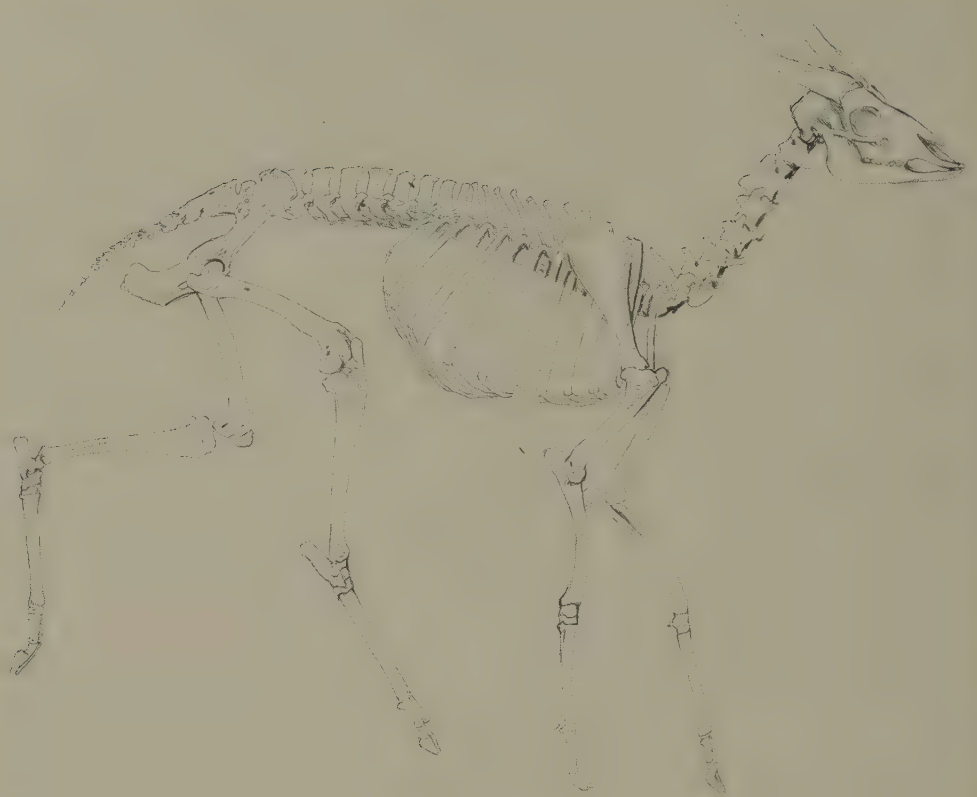
After giving birth and eating the placenta, the female leaves the young well hidden and on her visits to suckle eats the calf's dung. The calf does not usually change its refuge and it only begins to follow the mother when it is nearly four months old. Allsop thought that some regular associations of three females were probably a mother and two generations of young, so that associations might span more than one generation of young.

Sex ratios at birth are equal but estimates of adult ratios have varied widely, from 115 males to 100 females (Wilson and Child, 1964) to about 45 males to 100 (Dassman and Mossman, 1962a; and Waser, 1975b).

Mutual licking between parent and offspring is very common and I have seen mother and young making occasional play chases and running in circles, Ionides watched a wild bushbuck chasing and being chased by a guineafowl for ten minutes. The young male first sprouts horns at about ten months and by about 15 months has grown two 8 cm-cones, after which a keel begins to appear and a twist is apparent by the age of 18 months. At two years the horns are about 25 cm and have half a twist and by the time he is three years old they are often over 30 cm and well shaped. Infants are vulnerable to alert foraging predators and even chimpanzees and baboons have been seen to catch and kill the young. It is interesting therefore that larger bushbuck should not infrequently associate very closely with baboons. There are numerous reports of bushbuck picking up fruit falling from trees in which chimpanzees, baboons and other animals are feeding. I have watched a female bushbuck near Witu quite deliberately staying within a troop of baboons, keeping the same flight distances from me as the monkeys and, in spite of the open habitat, not concealing herself as might have been expected. Similar associations between bushbuck and baboons and with vervets have been reported from other areas (Elder and Elder, 1970).

Freezing and crouching are the bushbuck's usual response to an approaching predator. Kirby (1896) described a bushbuck that had seen him





"and at once lain down close to the bank, amongst the stones, with his head stretched out along the ground, and his horns consequently pressed flat back upon his neck. Crouched thus among the dark stones, the tops of which were rounded, and just about the height of his back as he lay down, his colour—darkened by the rain which was falling heavily—so exactly assimilated with that of the grey rocks around that he was practically secure from detection".

The cryptic appearance of a still, crouching bushbuck and the splendid conspicuousness of a prancing, displaying male provide a good illustration of the compromise between being seen and being overlooked. The role of cryptic behaviour in the tragelaphines in general has been discussed earlier (p. 72) and the bushbuck is perhaps the most successful "freezer" of them all, partly because of its small size. Nonetheless, it is more vulnerable to the leopard than to any other predator, a fact well borne out by the Kruger National Park records, (see p. 74).

The recorded predators of bushbuck are leopards, lions, hyaenas, cheetahs, wild dogs, crocodiles, chimpanzees, baboons, eagles and pythons. Servals and golden cats are other probable enemies. Bushbuck are exceptionally vulnerable to dogs once they have been put to flight, but sometimes allow a dog to pass them without moving.

In Kenya, a female that was pursued by wild dogs took refuge in a pool, swimming out to a clump of rushes. Males will sometimes defend themselves against attack and there are several records of men being killed by bushbuck during tribal hunts in Uganda (Blower, 1962).

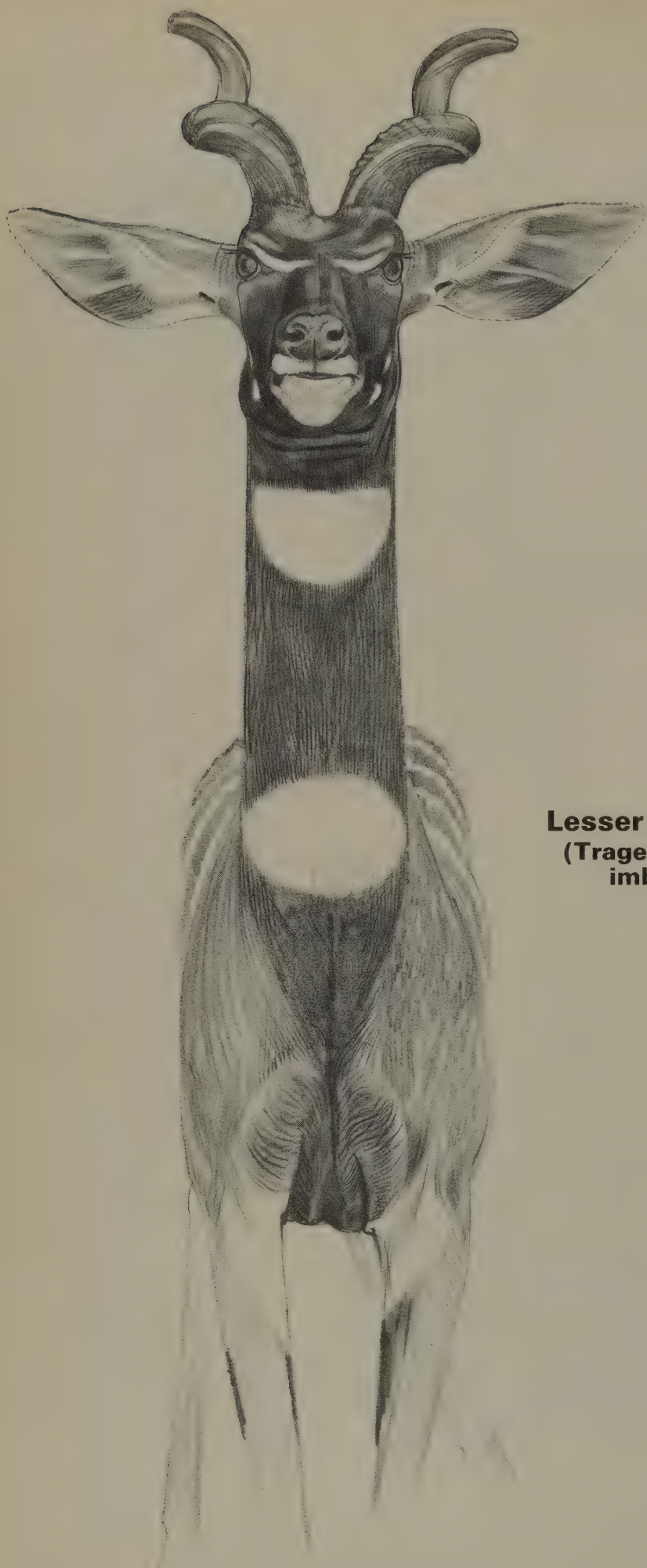


At one time the bushbuck provided the principal clothing for the Bagisu and some other tribes because the leather is supple, thin and sheds its hair readily.

Bushbuck dislike oxpeckers and Allsop thought they also avoided buffalo because of these birds. As a consequence they sometimes suffer from numerous ticks on the neck and ears, a site also favoured by flies.

In a West Uganda forest, joyful greenbuls, *Chlorocichla laetissima*, were seen picking insects off the back of a bushbuck.

They suffer from most of the common ungulate diseases and mortality from rinderpest was reported to be high during the 1929 epidemic. They have lived for over 12 years in captivity.



Lesser Kudu
(*Tragelaphus*
***imberbis*)**

Family

Bovidae

Order

Artiodactyla

Local names

Tandala ndogo (Kiswahili), O'siram (Masai), Gadams (Kiliangula), Esarich (Karamojong), Chaikoo (Ndorobo), Anderio (Somali), Nyamungata (Lwo), Nzaia (Kikamba).

Measurements
head and body

160—175 cm

height

100—110 cm

tail

26—30 cm

weight

92—108.3 kg males

56—70 kg females

horns

60—90 cm

Lesser Kudu

(*Tragelaphus imberbis*)

The lesser kudu has the most slender build of all the tragelaphines; proportions that are more likely to be adapted to its browsing habits rather than to locomotion, although this species is an exceptional jumper and often evades pursuit by leaping over tall bushes rather than skirting them.

The males are heavier than the hornless females and carry spiral horns of three relatively tight twists. Also the black and white markings on their face, tail and tawny-orange legs have greater contrast. The male's neck is augmented by a mane and the very short dorsal crest becomes a long tuft on the shoulder, which concentrates emphasis on the forequarters. The sleek, short-haired coat, which comes into great prominence during intra-specific displays, is marked with bold white patches in both sexes.

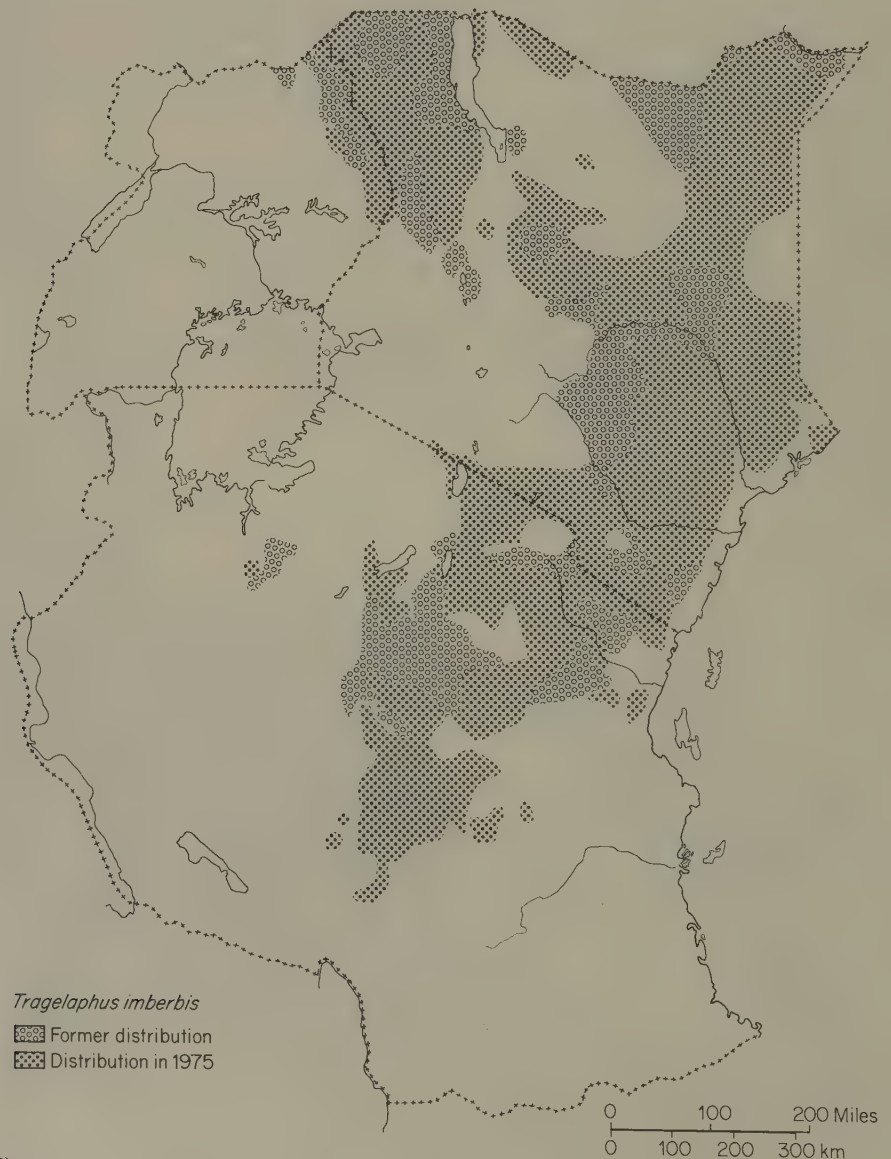
The colouring is an interesting example of cryptic adaptation in that the camouflage is most effective during the dry season. At this time the sandy grey colouring matches the grey branches of the thicket vegetation very closely and it requires a practised eye to see them when they remain immobile—their first response to a passing intruder.

This species is limited to thicket vegetation in the Horn of Africa, extending only as far as Uganda and south-east Sudan in the west and central Tanzania in the south. Where the climate becomes moister and the habitats thicker, the lesser kudu gives way to the bushbuck and there is only marginal overlap between these equivalent species (see maps). The lesser kudu apparently gains its advantage by an ability to do without water, while its stature allows it to browse higher. Individual ranges are also greater than

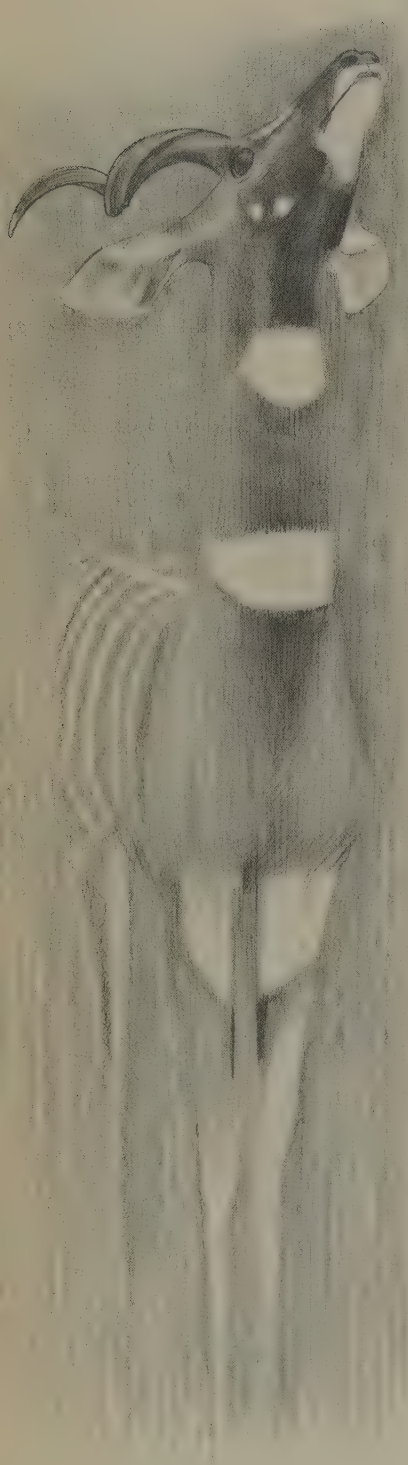


those of the bushbuck but like that species they are sedentary, which tends to restrict them to areas and habitats where the dry season is not so extreme as to deprive them of food and so demand large scale seasonal movements. Because reliance on crypsis is an inadequate strategy for survival in more open habitats, this is one of the limitations that define their niche (as it does for most tragelaphines) in terms of a certain minimum of low-level woody vegetation. The species is therefore tied to thickets in relatively dry habitats through its twofold dependence on this vegetation for food and cover.

The expansion of agriculture into marginal lands, the widespread felling and burning of trees for charcoal, massive clearance of vegetation against tse-tse fly or to plant sisal and groundnuts, and the recent heavy destruction of bush by elephants in parks has deprived this species of its habitat in many areas. On the other hand, overgrazing and erosion encourage the growth of thicket and it is possible that the species has actually benefitted from overstocking in parts of Karamoja and even Kondoia.







Lesser kudu probably depend on nocturnal grazing and succulents to get adequate moisture during the dry season, although they may visit water-holes while these are available. Schillings (1905) recorded finding the stomachs of lesser kudu full of *Sansevieria* fibres and Leuthold (1971c) has seen them eating the spiny succulent, *Euphorbia heterochroma*, during the dry season. In a detailed study of their food habits, Leuthold listed over 100 species of food plants. As well as being varied in composition, their diet shows pronounced seasonal changes. The animals become especially dependent during the dry season on evergreens supplemented by fruits of *Commiphora* and *Melia*, the flowers of *Anisotes* and the early sprouts of *Combretum* and *Cordia*; the dry leaves of Acanthaceae are also eaten. Leuthold rates *Calypotrothea*, *Euphorbia scheffleri* and *Salvadora persica* as the most important food plants in the Tsavo region. The buds, leaves and pods of various *Acacia* species, (including the hook-thorned "wait-a-bit", *A. mellifera*, often dominant in their habitat) are also common foods. Grass is eaten to some extent, particularly during the rains and Lamprey (1963b) reckoned two-thirds of their diet in Tarangire might be grasses. Leuthold noted that they are extremely selective about the species of grass and its growth stage. *Panicum deustum* was the favourite species in Tsavo.

One female living in the immediate vicinity of the Park headquarters at Voi was followed closely by Leuthold and he has shown (1974) how she was able to live on deciduous growth on the more elevated slopes during the wet season only to be more confined, in common with the other kudus in the area, to the low-lying evergreen belts during the dry season. Short-distance seasonal movements have been noted in the past in north-eastern Chua and Karamoja (U.G.R., 1935). However, hazards such as bush fires may force kudu out of their customary home range. Adamson (1972) remarked on the unusual sighting of lesser kudu 16 km from their normal habitat when it was burning, but the well-known attachment of this species to a small locality suggests that only severe ecological disturbance is likely to cause movements greater than 5 or 6 km. Leuthold (1974) found that the longest distance between two observations of the same individual, a subadult male, was 4.75 km. This class has the largest ranges (up to 6.3 sq. km) and adult females the smallest, averaging 1.8 sq. km. Adult male ranges averaged 2.2 sq. km.

The social structure has some resemblance with that of the bushbuck but the males appear to be less tolerant of one another and female associations possibly have greater cohesion. Leuthold (1974) described choice localities inhabited by a number of individuals as core areas of kudu activity. He thought that two or three females might sometimes form a nuclear group, as some female groups were reasonably stable over many months and might have originated as mother-young associations. Four or more adult males may share an area without obvious discord but also without mixing. There is no evidence of social changes with the seasons beyond those concerned with finding food. The association of younger subadult males with adult females is commoner than older ones, implying that subadult males become independent of their mothers gradually. The overall average group seen by Leuthold was three animals but he saw groups of over nine on 19 occasions and he once saw groups aggregated into a total of 24 animals.

While individuals living in the Sanu area might associate regularly, wandering strangers or neighbours from adjacent areas were very rarely seen by Leuthold.

The lesser kudu's method of sparring with its horns appears to reduce the danger of fighting. Heads are lowered and the horns are then laid lengthways against one another so that the twists easily engage and a see-saw pushing and twisting contest ensues. The few aggressive encounters seen by Leuthold occurred in the presence of females.

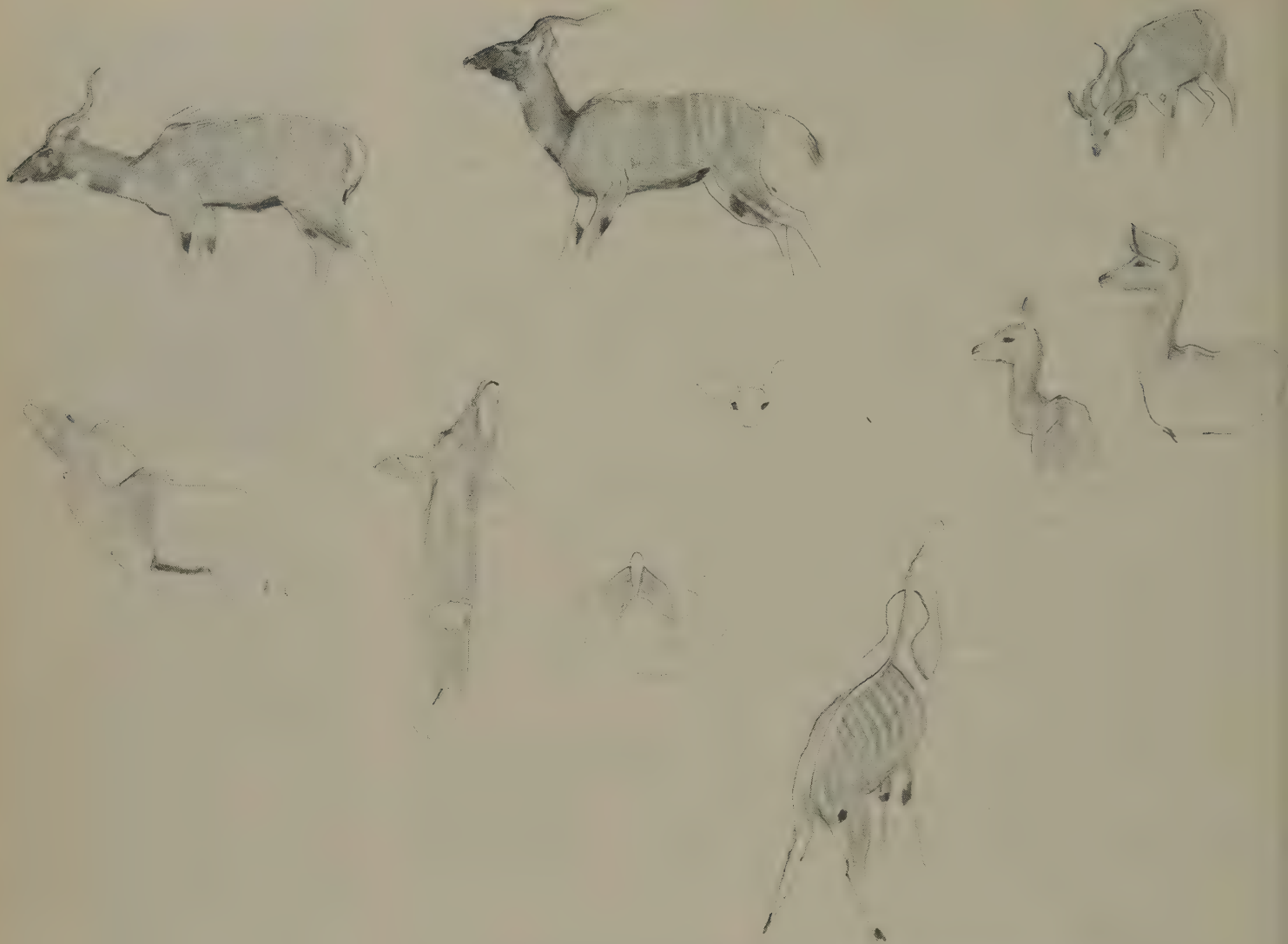
The normal gait is a level walk but when fleeing they may leap up to 2 m high, throwing the tail and hindquarters high in the air in a rocking horse gallop, sometimes uttering a harsh bark as they go. This may be uttered by either sex and does not necessarily cause alarm. Indeed, I have had the opportunity to observe what I took to be an important communicative function for barking. A subadult male was resting in the shade with two adult females. About half a kilometre away, in thick bush, a larger harem group was foraging quietly towards them from the south. The three were apparently alerted by the noise of their progress (and possibly by their scent, as they were downwind). After some minutes of attentive listening the three bounded off in a westerly direction, the male barking several times as he went. There was not the slightest sign from the immediate behaviour of the oncoming animals that the bark had had any effect upon them; they continued browsing without interruption but the entire group altered its drift from a northerly-facing direction to an easterly one, directly away from the departed trio.

When resting they prefer to stand or lie under thick bush where they are difficult to see. When watching an intruder, animals keep quite still but they make off the moment there is a sign of their having been seen.

Like the bushbuck, lesser kudu prefer to feed in the early morning and late evening but activity patterns may be altered somewhat by the seasons.



Courtship in this species is similar to that of other tragelaphines in that the male, having confirmed that the female is in oestrus, both pursues her but also halts her departure by standing broadside in front of her with head and nose lifted very high. Walther (1964a) described the female butting this obstacle to her escape, but the butts may turn to mouthing and then to a head-high staggering posture which elicits mutual chin and neck nibbling. As in other tragelaphine displays, the chin and neck chevrons appear to be attractive features and targets for mutual grooming. Sexual activity



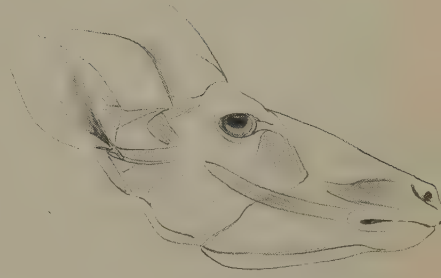
probably occurs throughout the year and gestation is approximately seven months. Rushby (T.G.R., 1945) thought there was a birth peak in central Tanganyika during May and June and reports from Karamoja have suggested there might be a peak there for May, with a possible second peak in November—December. Tsavo records suggest year-round breeding but Leuthold thinks that survival of the young is relatively low in the dry season, so a selective force might exist encouraging more births at other times of the year. Cover when the young are born could also encourage birth peaks. Leuthold described females secluding themselves after giving birth but they rejoin a female group eventually, particularly if the calf is lost.

Males grow up quite rapidly, their horns being about half as long as the ears by twelve months and nearly adult size before they are four years old.

They are taken by leopards, wild dogs, hyaenas, cheetahs, lions and smaller predators probably take the young; Leuthold (1974) reported a martial eagle killing a new-born calf. The species is known to have suffered from rinderpest in 1891, again in 1934 and also in the early 1950s.

This species is hunted for the sake of its handsome skin, particularly in Somalia (Funaioli and Simonetta, 1961) but habitat destruction is an even more serious threat to its existence.

They are popular and manageable animals in the confinement of zoos and parks. They breed readily and have lived up to 15 years. They have hybridized with bushbuck and sitatunga in captivity producing handsome intermediate forms.





Greater Kudu (*Tragelaphus strepsiceros*)

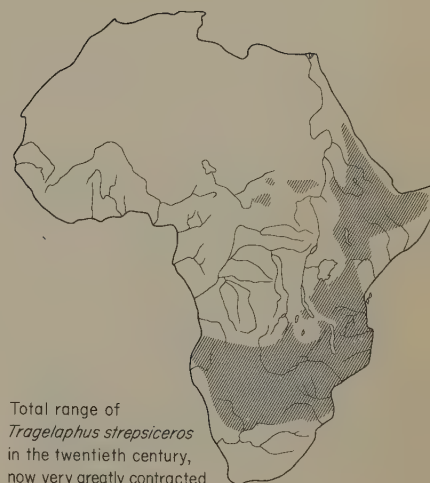
There can be few living mammals in which the difference between sexes is more spectacular than in the kudu, and the male's spiral horns are probably close to their mechanical limits in length and performance; yet this is an agile and even dominant species in wooded habitats where one might think the huge horns would be an impediment.

The persistence of such an extreme secondary sexual characteristic in a relatively successful species testifies to their importance in the kudu's social life, for horns are seldom used in defence against predators and both sexes are well known to hunters for their timidity.

The size and form of these horns has been considered within the broader context of the tragelaphines and their evolutionary radiation. The horns combine with visual devices to emphasize the size of the bull's forequarters and the depth of his neck; a mane up to the nape and a tasselled dewlap.

Both sexes are tall with a crest down the midline of the back. The colour is sandy-yellowish-grey with white body stripes and contrasting markings on the head and legs. The ears are very large and round. Very occasionally females are horned, bearing slender less-spiralled and shorter horns. The advantages of long necks and legs are obviously related to their bushy habitat in terms of browsing up to higher levels and of long-distance walking and occasionally leaping. Because bush tends to obstruct movement, kudu normally freeze or attempt to slip unobtrusively away from a disturbance, keeping a screen of bush between them and the source of danger. Occasionally bulls may plunge away with heads lowered but if really frightened they make the most astounding leaps that clear heights of 2.5 m with ease.

The kudu ranges through most of the drier areas of eastern and southern Africa wherever there is adequate low and medium level woody growth to provide browse and shelter. It is increasingly restricted to stony, hilly country because of cultivation or intensive hunting in the areas where better



Greater Kudu (*Tragelaphus strepsiceros*)

Family

Bovidae

Order

Artiodactyla

Local names

Tandala (Kiswahili and other languages), Inandara (Kijita), Ng'ikio (Kinyaturu), Wul Nyamungata (Lwo), Amakata (Karamojong), Malu (Kikamba), Nkuri (Kimeru), Saramai (Ndorobo), Sembelele (Luhya), Sirbey (Kalenjin), Lmaalo (Samburu), Emakate, Olmalu, Emaalo (Masai), Malee (Kiliangulu), Godir, Gothir (Somali).

Measurements head and body

220 (195—245) cm males

200 (190—220) cm females

height

135 (122—150) cm males

121 (100—140) cm females

tail

42 (37—48) cm

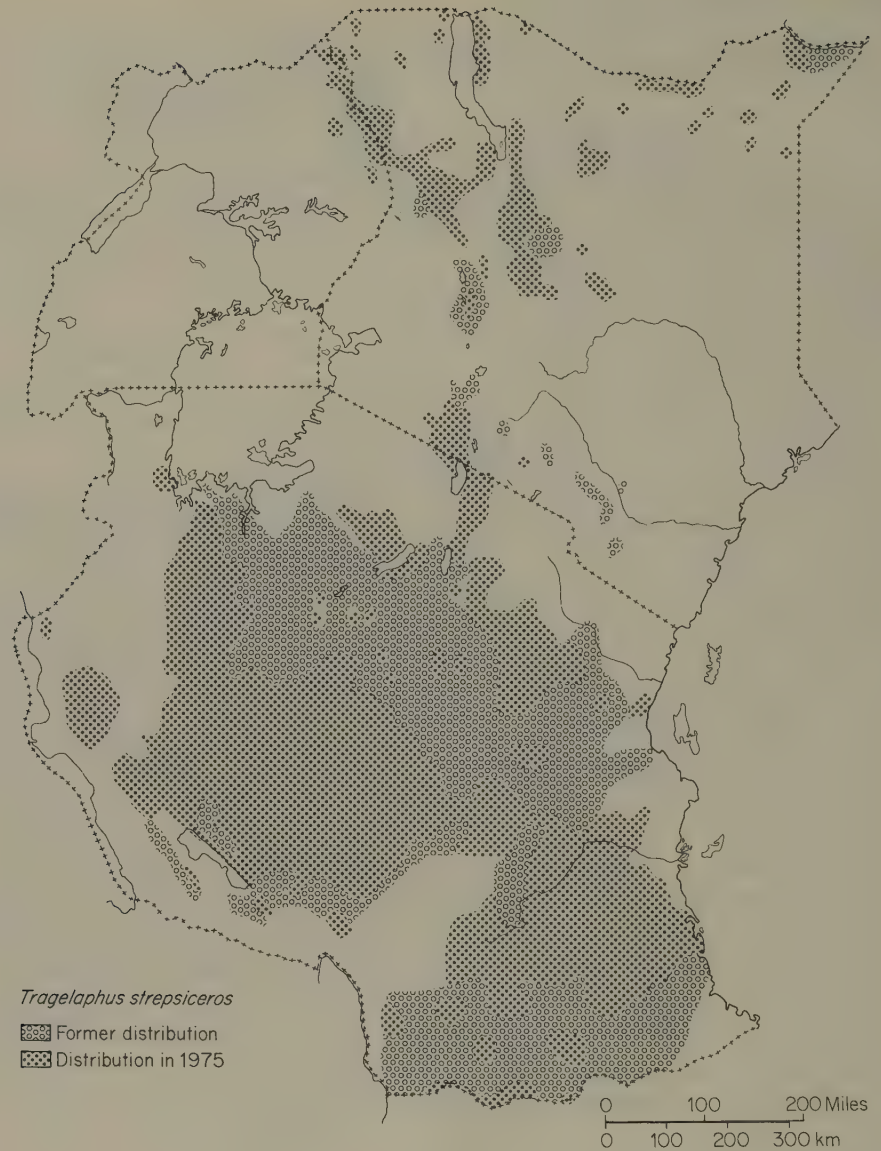
weight

257 (190—315) kg males

170 (120—215) kg females

horns

100—180 cm



soils or access to water have attracted people. As was discussed earlier, its range may also have been influenced by competition with other tragelaphines.

In central Tanzania they occur on all the escarpments of the Rift Valley and wherever there are rocky hills. They live in areas of thicket, particularly along watercourses, within the *Brachystegia* woodlands and also feed, particularly at night, on relatively open *Acacia-Commiphora* hard pans. During the dry season they may enter riverine evergreen forest and thicket.

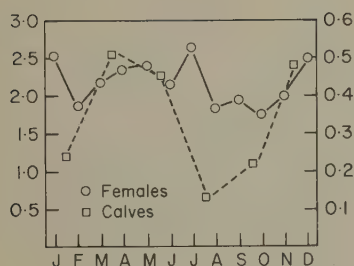
Because of the very marked seasonal changes in its habitats and because many of its food plants are deciduous, the greater kudu is often forced to change its diet, the pace and routine of its movements and even its habitat with the seasons. At Shinyanga, Harrison (1936) recorded 36 species of food plants and the frequency with which they were eaten and other studies on its diet have been made since. The Shinyanga records can be augmented

with some from other areas, namely, *Aloe*, *Calotropis procera*, *Croton gratus*, *Bridelia*, *Olea africana*, *Rhus* and *Zizyphus*. In settled areas they are attracted to cultivation by the hedge plant *Euphorbia tirucalli*, by the prickly pear, *Opuntia*, and the castor-oil plant, *Ricinus*. At times they eat a lot of fruit, particularly those of *Acacia* spp., *Balanites*, *Dichrostachys*, *Grewia*, *Lannea*, *Parinari*, *Sclerocarya*, *Pseudolachnostylis*, *Piliostigma* and *Solanum campylacanthum*. They very seldom graze and then only on fresh green grass. They occasionally use their horns to break branches.

Such large antelopes require proportionate quantities of food and stomachs have been weighed out at 30–38 kg (Wilson, 1970). Hofmann (1973) has remarked on the adaptation of this species to rough and chemically aggressive foods, manifested in a heavily keratinized reticulum; he has also noted the rapid passage time of food and found capacities between 27 and 71 litres in the ruminoreticulum with as much as 21 litres of food. To obtain such quantities is relatively easy in the wet season but it is more difficult during times of drought. At the height of the southern dry season in September, Owen-Smith (1975) found kudu spending 85% of the day foraging at the rate of 312 feeding minutes in 100 paces, whereas in December, during the rains, only 69% of the day was spent foraging at the more rewarding rate of 460 feeding minutes in the same number of paces. The animals moved very little at this period and stayed in lush vegetation near watercourses. Nocturnal feeding took up 40–50% of the night and similar differences in seasonal activity patterns could be predicted.

The wide dispersal of kudu during the wet season not only scatters individuals but also has the effect of separating the sexes. Observers in both eastern and southern Africa have remarked on the periodic seclusion and elusiveness of adult males. Both north and south of the equator young tend to be born in the earlier part of the rains and rut follows some three months later, thus temporarily uniting the sexes. After an absence of five months or so, Owen-Smith (personal communication) identified bulls returning to the same area they occupied the year before: several bulls encompassed the home ranges of two or three groups of females. Their areas of occupation overlapped but the largest bull merely gave a lateral display when another male approached and gave chase only if the other attempted to join a female. Male kudu are highly localized in their movements at this time. It is probably seasonal scarcity of food that puts a fairly tight upper limit on the numbers of animals that can associate together. Female groups average five or six animals (with a normal range of two to fifteen); typically they include several adults with immature offspring of both sexes. From time to time larger groups may break up and smaller ones amalgamate and it is not known how lasting or consistent associations are. Owen-Smith (1974) has evidence for groups retaining discreet identities from one year to the next and he saw different parties mingle temporarily only to separate out into their own units again. He thought female dominance relationships were suppressed or absent.

Heavily pregnant cows leave their groups to give birth but they rejoin their former associates over the two or three months that their calves spend lying out in hidden retreats. Records of average numbers in female groups at Loskop Dam, South Africa, showed a drop during the birth season



Average number of females in groups (exclusive of all-male groups); and number of calves with average female. (After Underwood, 1978.)

followed by a monthly rise in average numbers, peaking a month after the end of the rains (Underwood, 1978). The numbers then dropped off steeply and reached their lowest at the end of the dry season before rising again with the rains (see margin). Males follow a different social pattern. After the rut, which occurs at the end of the South African winter, and during the August–September “second rains” north of the equator, the adult and subadult males tend to aggregate in bachelor groups numbering between two and ten animals. Owen-Smith thought that membership of these all-male groups is transitory and without consistency, and scattered observations suggest that there may be a decline in numbers as the dry season makes group feeding more and more difficult. With the arrival of the rains there is a widespread dispersal and Owen-Smith (personal communication) saw the brief appearance of strangers and the striking absence of formerly resident bulls as evidence that the first half of the rains led to much movement, particularly by males avoiding areas where females were concentrated. There are reports of very large aggregations of kudu in the Namib region (i.e. Gaerdes in Jungius, 1971a) but they are unexplained and clearly very unusual.

Home ranges have been investigated by Owen-Smith using telemetry. He found two female groups encompassed 3.6 and 5.2 sq. km respectively. The centres of home ranges were spaced out but there was extensive overlapping. Two male home ranges measured 11.1 and 11.2 sq. km.

Overall sex ratios vary from locality to locality and Mentis lists ratios from 15 males to 100 females and 75 males to 117 females; however, on average there are about 2.5 females for every male. Densities vary widely and Owen-Smith calculated 1.9 to 3.2 per sq. km in his two South African study areas.

Solitary habits put males at greater risk and the younger animals are probably the most vulnerable but male movements and mortality patterns have not been studied.

Owen-Smith (1975) noted that all the males in his localized study population associated together at some stage and he remarked that this must have provided opportunities for individual recognition and the establishment of stable dominance relationships. Where there are differences in age and therefore of height and horn length visual displays are an adequate assertion of dominance but, where males are equally matched, encounters are more likely to culminate in a fight.

It has already been remarked (p. 29) that there is a relationship between a tragelaphine's proportions and the length of its horns and between their shape and fighting technique. In the kudu's case, the tallness has a direct bearing on the length and span of the horns, which are 100–180 cm from base to tip end, with a divergence at the tips as variable as 23–132 cm. Because the horns have to shield the body of a sparring male there is a relationship between the area of animal that is exposed in a fight and the volume of space within which the horns can engage. Kudus do not rush upon one another but stand on all fours and engage the spiralling surfaces of their horns to make a firm link-up against one another. The rivals push and attempt to throw one another off balance. The wide open twists pass through two-and-a-half turns in an adult and they provide both engaging surfaces



side profile -
intance.

note the hump of
the neck & chest
on the foreleg



on the anterior curves and holding or checking bars in the posterior concavities. The first convergence of the horns is particularly conducive to mutual locking and also limits the thrust of an opponent's horn tips by tending to trap the opposing horns beneath the second outward flare. These lateral oscillations of the spiral not only encourage a symmetrical link-up of opponents and spread out the defensive "shield" but also enlarge, particularly from the frontal aspect, the area of "target" against which the rival must direct his attack. Very occasionally the spirals interlock and the animals are unable to disengage. Such combatants die and I have seen the skulls of such a pair in Central Tanzania.

Fighting is generally unnecessary because lateral displays determine rank. During these ceremonies a toss of the horns may be accompanied by tongue-flashing.

The physical structure of the two diverging spirals is related to the kudu's technique of horn wrestling but the horns can also have visual properties which, while incidentally enhancing their roles as symbols of rank among rival males, may have some impact on females, for the visual element of the male's display appears to be most important in courtship. (Indeed, if there were any tendency for females to accept males with the largest horns as mates, this would certainly favour retention of maximum-sized horns on the basis of their display value alone.) Females are not normally touched or prodded by the male's horns, although intimidation plays its part in the kudu's courtship no less than in most other antelopes.

Courtship rituals which resemble those of other tragelaphines have been described by Walther (1964a). Once the male's interest in a female has been aroused he pursues her closely and tirelessly with head held forward and horns laid back. His head is held close to her flank or shoulder and courting bulls have been described as making whining grunts or clucking noises. At this time secretions from cheek glands may be transferred to the female. When he can, the male gets his head across the female and pushes her neck down with his, which generally brings a receptive female to a halt. This symbolic domination may cause the hairy dewlap to brush over her face and neck like a soft curtain. The male may also attempt to halt a fleeing female with a lateral display in which the head and chin are lifted, to which the female may respond by also raising her chin; this is generally followed by mutual nibbling and the necking ritual. Once the female is wholly submissive, the male rubs his chin and neck along her back and finally mounts her.

Although mating is very largely restricted to the earlier part of the dry season or the late rains, some scattered birth records show that sexual activity can take place at other times. In Karamoja males have been seen with female groups between August and December and most mating is thought to take place in September.

The gestation period is close to nine months, which ensures that most births in all regions take place during the rains, when there is shelter for the young and moist food for the lactating mother. Underwood (1978) noted that the arrival of the rains in southern Africa coincides with the period of greatest demand on cows which are in advanced stages of pregnancy.

Left: development of spirals. Top to bottom: approximately 1, 2, 3, 4 and 5 years.

The young remain in their hiding places for four or five weeks before accompanying the mother for the morning, gradually increasing the time together until by three or four months they stay together all day. Once in a group and with other young kudus they can be very active and playful. Body growth is rapid and the young are fairly independent of their mothers by the time they are six months old. Males have grown a full twist to their horns by the age of two years and the total spiral of two-and-a-half twists is reached between four and four-and-a-half years. Captives have lived over 15 years but wild animals are unlikely to live more than 11 to 13 years.

Mothers probably resemble elands (p. 136) in communicating and regaining contact with their young during the lying-out period by means of the voice. Like all tragelaphines the adults sometimes utter very loud barks but are normally silent.

The kudu is known to be highly susceptible to rinderpest and it has been suggested that recurring epidemics depressed populations in Kenya.

Lions, leopards and wild dogs have been recorded killing kudu and spotted hyaenas probably hunt them in some areas. Cheetahs occasionally kill juveniles and females and there is even a record of one bleeding to death after having been attacked by a ratel.

Kudus are hunted in all regions where they occur and are even cropped on a regular basis in southern Africa. They have retreated or disappeared in parts of their range where charcoal burning, the felling of thickets and cultivation have deprived them of food and shelter.

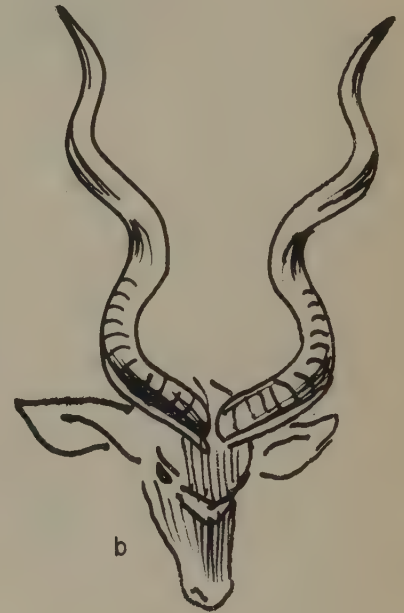
Damage to crops and a taste for their excellent meat are common incentives for hunting, and male horns have been a prized trophy in Africa for many centuries. The Wanderobo use them as containers for honey and many other tribes value them as musical instruments for ceremonies and dances. They are also a dwelling for powerful horn-spirits and are sometimes worn or carried by performers in rituals. They also symbolize male potency and it may be this as well as their beauty that underlies their popularity as trophies. Finally, the metaphysical symbolism that such horns have had for some African cultures has been described by Fagg (1973).

"Tribal cultures tend to conceive things as four-dimensional objects in which the fourth or time dimension is dominant and in which matter is only the vehicle, or the outward and visible expression of energy or life force ... of all the sculptural forms given to the concept the most striking is the exponential curve described in the growth of the horns of rams and antelopes ... such curves are by their nature a record of growth in time and sculptures based on them, though having only three dimensions, convey the fourth as well."

The kudu's horns are of course splendid and tangible tokens of growth and curved or spiral horns seem to have excited widespread aesthetic responses in human cultures.

Introverted preoccupation with the symbolism of horns within human society has overridden interest in their purpose within the life history of the animal. We still have a very incomplete understanding of the evolutionary processes that produced such perfect geometric forms.

Right: Spirals in greater kudu. Top: parallel; middle: normal; bottom: splayed.





Derby's Eland
(*Taurotragus*
***derbianus*)**

Family

Bovidae

Order

Artiodactyla

Local names

Gogwell (Nuer), Bwobwo (Madi and
Lugbara).

Measurements

head and body

290 cm (approx.) males

220 cm (approx.) females

height

150—176 cm males

150 cm (approx.) females

tail

55—78 cm

weight

450—907 kg males

440 (approx.) females

horns

80—123 cm

Derby's Eland (*Taurotragus derbianus*)

This very rare animal was reported to have been eliminated in the Uganda part of its range during military operations in 1970.

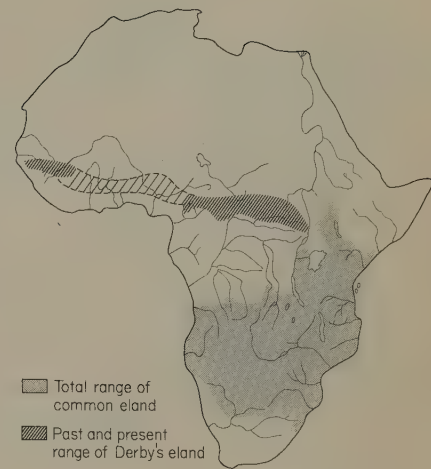
As a nomadic animal there is some hope of its recolonizing some of its former range if its habitat remains intact but West Madi has always been too remote to excite much interest in protection. Likewise, the species has disappeared from the greater part of its former range without attracting much notice.





The morphology of *T. derbianus* is interesting because it illustrates the course of evolution taken by the eland. If this species is not directly ancestral, it certainly derives from a more primitive type than *T. oryx*.

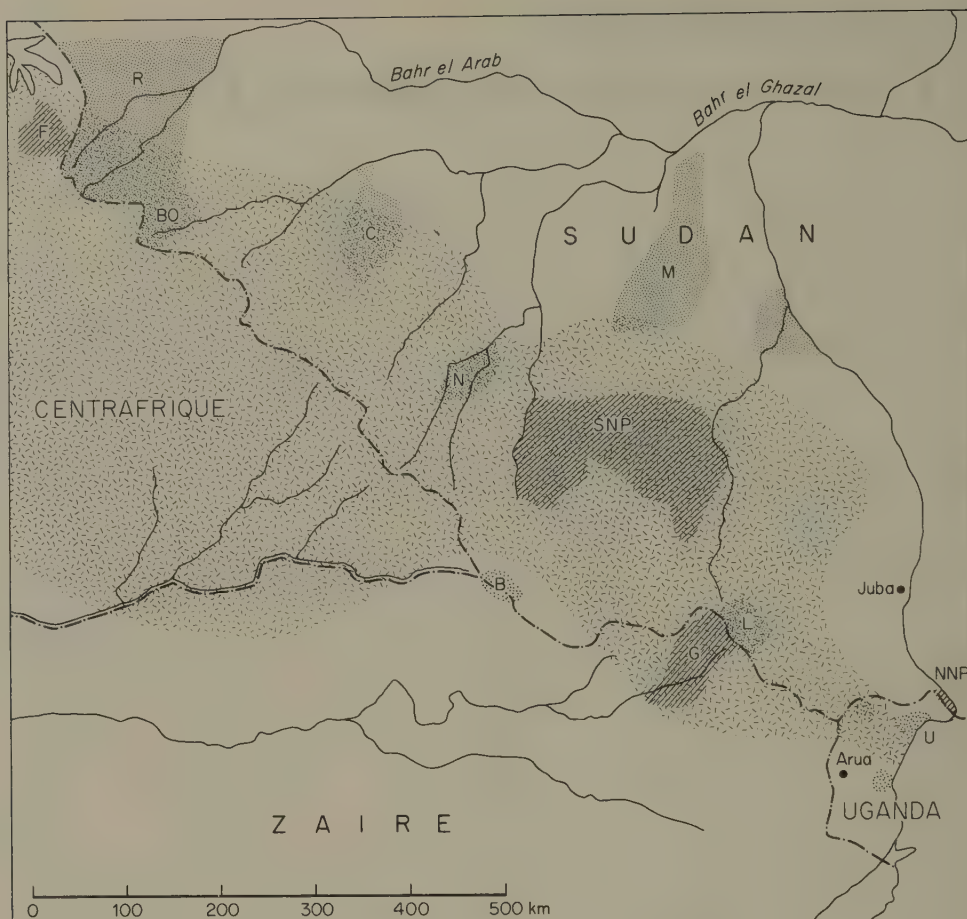
The common eland has numerous features in which it differs from other tragelaphines. Some of these features can be correlated with its special adaptation to a nomadic life in more exposed habitats and resort to a more social way of life (see pp. 130–134). Both sexes possess horns but the gregarious females of *T. oryx* have long slender ones while the males have massive short ones. It is clear that the ritualized component in male horn display has declined and the strength of the horns is tested directly through pushing and twisting contests, giving greater advantage to the stoutest, shortest horns. By comparison, *T. derbianus* tends to have longer and more slender horns. The widely divergent tips and a more open spiral in male *T. derbianus* as well as their behaviour suggest that the elands have derived from a form with true display horns. Hair on the forehead of Derby's eland is differentiated in colour but it has not become the dense mat found in the common eland. The peculiar form of dewlap and marking of the neck suggest that Derby's eland is a species transitional between a horn exhibitionist and the "parade bull" eland. In the latter, emphasis is more on body mass and weight; in the former type, of which the greater kudu is an extreme example, mane, dewlap and colouring serve to emphasize the height of the head and horns so that the neck becomes a visually distinct unit from the body. Even the ears play a part in this transformation; hearing is obviously more important for an animal living in cover than for one living in the open, but the large pinnae also serve as signalling devices, which focus attention still more on the head. In the common eland pattern has been suppressed on the greatly reduced ears.

Derby's eland, instead, has very large conspicuous ears and a dewlap that starts beneath the chin. As if symbolic of its dual emphasis, the dewlap has two tufted points, one beneath the jaw, the other at chest level. A black collar at the base of the neck links the black tufted dewlap with the vestigial mane and boldly separates the body unit, whereas it is the shoulder that is emphasized in the common eland.

These differences have some correlation with behaviour. In the course of preparing a thesis on the ethology of *T. oryx*, Underwood (1975) compared a pair of captive Derby's eland with the common species. The animals generally stand more erect and this finds ritualized expression in the males'



-  Total range of *Taurotragus derbianus* in Uganda, South Sudan and Zaire, with conservation areas indicated.
 Established National Parks
 Reserves and proposed conservation areas
 National boundaries
 NNP: Nimule National Park;
 SNP: Southern National Park;
 G: Parc National de la Garamba;
 F: Parc National André Felix;
 R: Proposed Radom National Park;
 BO: Proposed Boro Reserve;
 C: Chelkou-Ashona Reserve;
 N: Numatina Reserve;
 M: Proposed Meshura Reserve;
 B: Bangangai Reserve;
 L: Proposed Lantoto National Park
 U: Uganda conservation areas. See Vol. III B pp. 107-119.



“proud” neck displays with lifted head. The female has also been seen to lick the white bar on the male’s throat and also his hairy dewlap. Rubbing a partner with the forehead and chin is also more pronounced a behaviour of *T. derbianus*. Both species of kudu commonly point the nose vertically upwards in threat and Underwood (in lit.) saw this in Derby’s but never in the common eland and he remarked that courtship is more elaborately ritualized.

Originally ranging throughout the *Isoberlinia doka* woodlands, the shoots and leaves of which provide much of their food, Derby’s eland are probably more exclusively browsers than *T. oryx*. Roosevelt (1910) summarized his experience of them:

“They usually went in herds, but there were solitary bulls. We found that they drank at some pool in the Koda before dawn and then travelled many miles back into the parched interior, feeding as they went; and after lying up for some hours about midday, again moved slowly off, feeding. They did not graze but fed on the green leaves . . . they broke branches two or three inches in diameter and seven or eight feet from the ground, the crash of the branches being a sound for which we continually listened.”

They will, however, feed on freshly sprouted vegetation after a burn and, as early as 1925, *T. derbianus* were noted moving east out of the Belgian

Congo between January and April, a movement that Pitman thought might be governed to a great extent by grass-burning. During February herds of 30 and 60 animals were noted in this part of the West Nile district but they were nearly all cows, and adult bulls were absent. Bulls are solitary or gather in small groups and Ionides (1965) noted as many as five bulls resting in shade together. Up to 1950 Derby's eland was thought to be a frequent but seasonal visitor to Uganda, wandering as far as Dufile on the banks of the Nile. Records and numbers increased around 1950, herds of 60 being seen in June and July and smaller herds in April and August. *T. derbianus* was believed to be permanently resident in Uganda along the Ilengwa range in West Madi, while there was regular annual movement into the Midigo area of West Nile from the Sudan. During the rinderpest outbreak in 1955 four carcasses of giant eland were found at Loreze, one being a large bull, another an old cow and two young.

Rinderpest may have reduced numbers generally since only a pair were seen on the Ilengwa range during the following two years, but slowly numbers increased again in the early 1960s. The migrants into Uganda were the most south-eastern part of a population that in 1950 occupied a belt of habitat averaging 125 km in width but stretching nearly 1,000 km to the west of the Nile (Molloy, 1955).

This species seems to be exceptionally firmly tied to its woodland habitat, a limitation that is not apparent in *T. oryx*. Considering the possibility that it may be the contemporary representative of an earlier stage in the evolution of elands, it is a worthwhile candidate for detailed study. In spite of being a much sought-after trophy for three-quarters of a century, even the most elementary observations on its ecology and behaviour have not been recorded.

The principal remaining reservoirs of this species are in the southern Sudan and the three Cameroun reserves, Bourbandjidah, Benone, and Faro, where Flizot (1962) estimated a population of 4,000.





Eland
(Taurotragus
oryx)

Family
Order
Local names

Bovidae
Artiodactyla

Pofu, Mbunju (Kiswahili), Entengo (Luganda), Entamo (Runyoro), Ekishwaga (Runyankole), Abwori, Abuor (Lwo), Egwapet (Ateso, Karamojong), Morju (Kiliangulu), Roganiet (Sebei), O'sirwa (Masai), Damau, Singoita (Ndorobo), Oyepet (Toposa), Ewapeti (Turkana), Aalwein (Somali), Mpoku (Kinyiramba), Mpofu (Kizigua), Igalu (Kitaita), Thirua (Kimeru), Thiruai (Kikuyu), Kubragan (Saboet, Elkoni), Namu (Kikamba), Surua (Samburu), Isiruri (Majita), Esakari (Luhya).

Measurements
head and body

300 (250—340) cm males

230 (200—280) cm females

height

150 (135—178) cm males

135 (125—150) cm females

tail

60 (54—75) cm

weight

690 (400—942) kg males

450 (390—595) kg females

horns

60—102 cm

Eland

(*Taurotragus oryx*)

The eland, like other heavy animals, shows signs of being modified by the demands of its large size. It has a shorter more robust neck and legs than its immediate relatives, which gives it a more bovine look. Nonetheless, it is unmistakably a tragelaphine antelope and is considerably taller and more agile than a cow or a buffalo.

There are few mammals in which the size and appearance of the sexes differs so greatly. An old male can achieve weights not far short of 1,000 kg and may be twice as heavy as an adult female; furthermore, males continue to increase in weight over a very long period. As it becomes heavier, the male's neck and shoulders darken from tan to grey and the dewlap enlarges until it is like a curtain hanging from the throat to below the level of the knees, which gives a grotesque visual emphasis to the forequarters. The male's horns are thick and tightly screwed. The hair on its forehead and nose changes its length and colour from time to time. From being short and sandy the hair becomes chestnut and then black extending down the nose into a double tuft as it develops. The skin in this area is thick and may be glandular; in any event it sometimes overhangs and distorts the upper lids of the eyes. Hillman (personal communication) has seen a black double tuft decline to a single chestnut tuft and this reversibility implies that the development of the tuft is under hormonal control.

The concentration of weight on the forequarters in elands probably influences the greater size of the forehooves. The female is more slender with long, thin horns and is well marked with white stripes on the fawn body. The midline carries a short dark mane and the throat has a tufted dewlap that is very much smaller than that of the male and placed further up the neck.

Both stripes and dewlap tuft differ from one animal to another, which makes visual recognition of individuals easier, not only for the human observer but presumably for the eland as well.

They give every sign of being sharp-sighted over considerable distances. Their hearing is also good but the pinnae of their ears are greatly reduced in comparison with those of bongo, kudu or buffaloes.

In contradistinction to their great bulk there is a gross disproportion to the mouth and muzzle, which is small and pointed in the eland instead of being blunt and broad as in cattle and buffaloes. Not only is the mouth different but the teeth and small jaw muscles betray a soft diet, while the digestive system, which has been described by Hofmann (1973) as that of an intermediate type, is adapted to a low fibre, high protein diet.

Wherever there are strong seasonal changes (which is the case throughout a large part of the eland's range) soft browse is frequently ephemeral or scattered and eland are therefore nomadic, moving whenever necessary from one distant pasture to another. Even in the course of a single day's foraging they frequently cover a large area. The disproportion of the muzzle is therefore symptomatic of a selective diet which, because it needs to be satisfied



Variations in frontal tuft colouring and horn shape in eland bulls from East Africa.



in quantity, demands mobility. Cattle and buffaloes which graze from a wider choice of vegetation and so need to move less, have relatively shorter legs than the eland.

Such differences in diet and natural history can be correlated with differences in the gross proportions of this species vis-a-vis the bovines but the question of morphological differences between male and female eland has been discussed in the tragelaphine profile (p. 80).

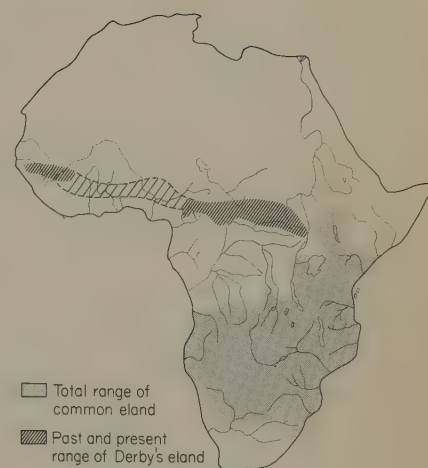
The eland originally ranged throughout the southern savannas and woodlands. Derby's eland, although inhabiting a narrower range of habitats in the northern savannas, used to monopolize the *Isoberlinia* woodlands in this region of Africa. Through most of the eland's extensive range the changes wrought by the seasons demand a nomadic existence in such a large social browser and the females, in particular, use distinctly different habitats and

change their diet according to the seasons. Observers from widely separate localities have described similar patterns of movement. Selous (1899) recorded hundreds of eland gathered together during the wet season. Wilhelm (1933) recorded the formation of similar congregations on open areas of the Okavango region during the rains with the animals dispersing into thicker vegetation to spend the dry months browsing off the trees. Shortridge (1934) also noted that small groups were normally scattered but temporarily associated in larger numbers during and after the rains. At Shinyanga, Harrison (1936) recorded congregations of up to 80 animals moving into an area for a few days and then deserting it. He recorded that the main attraction for herds on the alluvial plains during the wet season was small herbaceous plants and herbs and he quantified the seasonal changes in their diet (p. 80). He remarked that when some plants such as *Commelina* were abundant they were such an attraction that eland could always be seen feeding on them. Other favoured plants are *Ipomoea* (including their tubers), *Vigna trilobata* and *Hibiscus*. The similarities in the choice of browse by eland and kudu are shown in Harrison's figures (p. 80).

Combretum woodlands are particularly favoured browse. Early flushes of grasses such as *Themeda*, *Setaria*, *Panicum maximum*, *Sorghum arundinaceum*, *Phragmites* and *Vossia* often attract large congregations of eland and it was perhaps a strongly seasonal bias that gave Lamprey (1963b) his 70% grass diet sample for Tarangire. Stewart and Stewart (1970) and Wilson (1969b) recorded eland eating more grass during the wet season than in the dry. Hillman found an interesting sexual difference in the amount of grass taken during the wet season. Because the males venture less into the open country than the females, their diet remains more consistently one of browse and herbs. The pods of various acacia trees are eaten in quantities, particularly during the dry season, while the eland shelter from the sun in the shade of *A. tortilis*. The facilitation of seed dispersal achieved thereby was remarked upon in Vol. I (pp. 33—36). Eland sometimes use horns and hooves to break away the branches of trees and also push themselves into shrubs and bushes so that intensively used areas often show signs of severe damage. The use of horns for breaking branches which are then nibbled seems to be learnt, since it is sometimes very common in bush country after fires have scorched all the ground level vegetation; yet is scarcely ever seen in other areas where food is within easy reach. Otherwise, horning of vegetation is primarily a male display although females occasionally do it as well.

Eland use their hooves to dig up roots and Wilhelm (1933) reported them digging up *Ipomoea* tubers; he also found quantities of mineralized earth in stomachs. Visits to salt licks are common and on Kilimanjaro the Shire eland go as high as 5,000 m for soda licks near the snowline.

Seeking shade and selecting moist foods are amongst the strategies of the eland in dealing with drought and it can do without water for relatively long periods. Physiologically the eland has a high metabolic rate (Rogerson, 1968) and it excretes dry faeces and a highly concentrated urine which has a high urea content because of the eland's rich diet (Taylor and Lyman, 1967). Studies of protein synthesis in cattle have shown that urea is better used and converted by cattle, but their ability to cope with drought is inferior to the eland's.



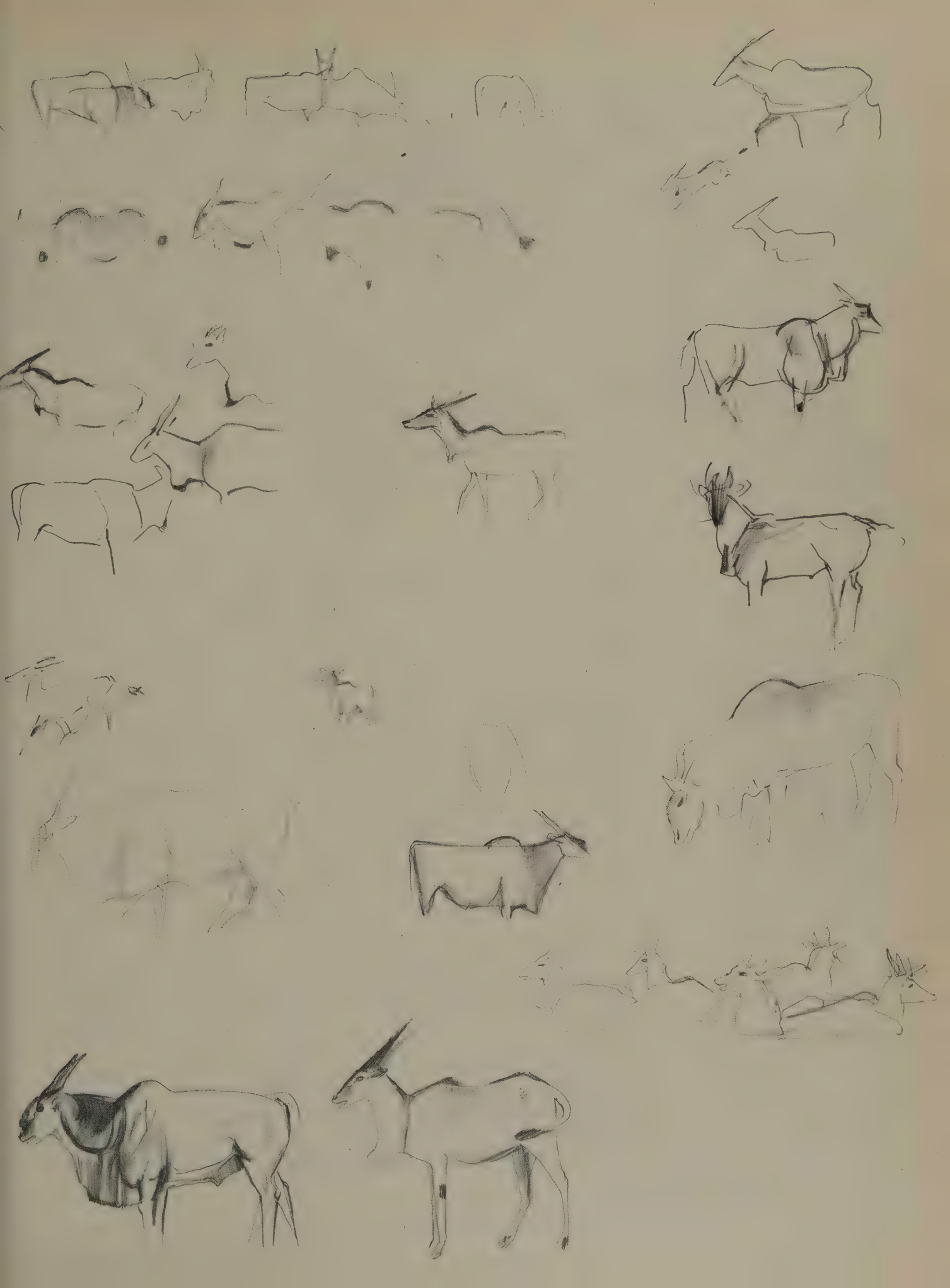
Unlike other antelopes, eland do not congregate round water, or disperse across the plains in the wet season in smaller groups. On the contrary, large groups forming during the rains in open country drew puzzled comments from many of the early naturalists and hunters. Shortridge (1934) remarked on how groups may be of one sex only or entirely half-grown. Selous described seeing an isolated group of 50 calves all of similar ages. Hillman (1974) has pointed out that not only do the young tend to associate in large numbers but that all herds with young are consistently larger at all times and he has suggested that the trait has evolved as a defensive tactic against predators. The mechanism for these larger associations seems to lie in the intense mutual attraction of calves, while the mothers, as Moss (1975) puts it, "just have to go along." The origins of this attraction are of course unknown but selection might have fixed an essentially defensive trait and provided thereby one of the more lasting adhesives to draw individual eland together. The close association of calves begins at an early age and, in terms of time spent together, calves are more attached to other calves than to their mothers. Even when drought is at its worst and scarcity of food forces large groups to fragment, the young maintain their attachment to others of their own size. They also contrast strongly with adults in grooming and licking one another, whereas adults have minimum physical contact. However, this does not leave its mark in the form of lasting bonds between individuals in adult life. Male associations tend to be of dissimilar ages, which may be due to the potential for conflict between well-matched bulls.

If the close association of juveniles is an extension of defensive bunching, their preference for animals of their own class may simply reflect the best strategy for survival. On their own, mothers may be indifferent to the fate of calves but, once alerted and bunched in formation around the young, they may join other adults in a concerted attack, even on large and dangerous predators. The survival of individual calves would be less well served by their looking directly to their mothers for protection than by maintaining cohesion as an age group and relying upon the larger animals to defend the entire herd.

It is only during the two weeks of concealment that a calf is totally dependent on the mother. After that calves may even suck mothers other than their own and the mother's role as a companion is supplanted by the other young animals in the nursery group. At this early age the young eland is introduced into a social milieu, the essential characteristics of which are carried on into adult life.

Hillman's correlation of larger juvenile assemblies in more open habitats is a significant one; for at a phylogenetic level it suggests that calves have been the class most immediately affected by the eland's evolutionary shift into more exposed habitats and that selection has elaborated on the changes wrought on this class. What might appear to be a temporary expedient has actually provided a strategy by which independent animals can gain the benefits of herd life without forming ties. Any form of permanent bonding would put a premium on refinding lost partners and so would waste energy and diminish the animal's capacity to disperse according to the vagaries of the food supply.

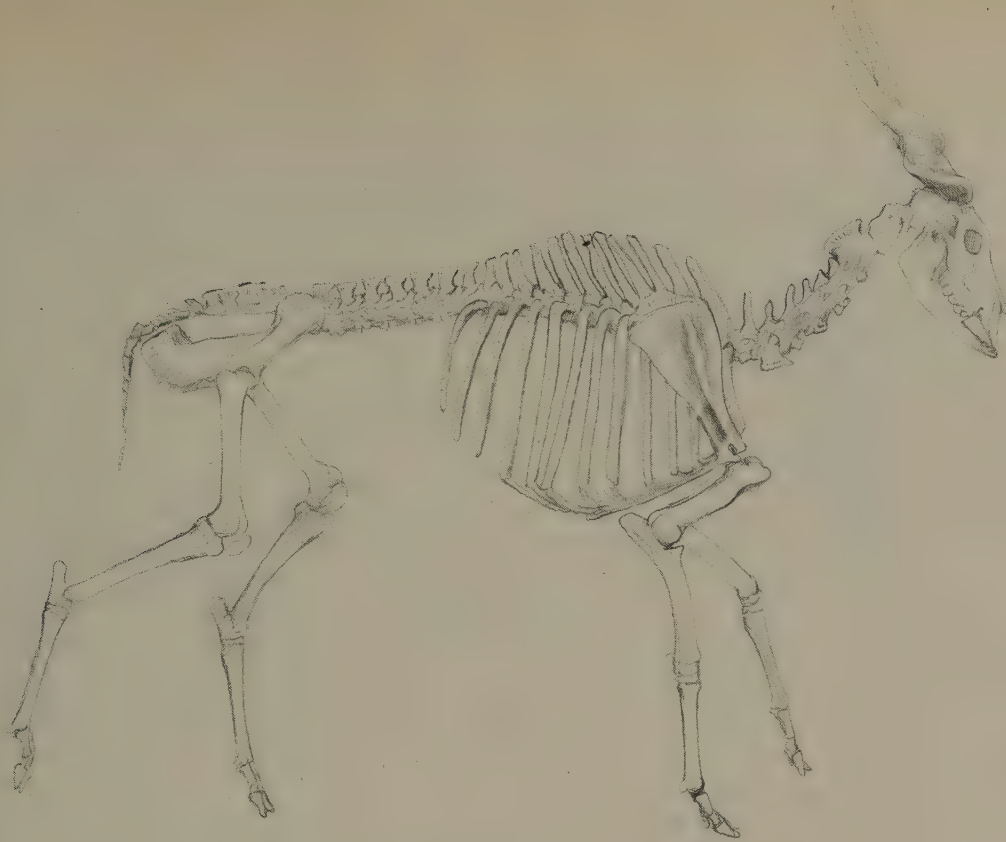
Calves grow very fast and this characteristic ensures not only that they





soon get through their vulnerable infancy but that their associations tend to include animals of widely disparate size. Given this characteristic and the fact that membership is seldom stable, juvenile groups are effectively ranked by age and relative development. The continuous increase in the male's weight, his changing colour and progressive growth of the dewlap imply that the principle of seniority by age and size is extended in the male eland to embrace, if not the total span of life, at least the larger part of it. The extraordinary physique of the males may therefore be a manifestation of a hierarchical principle with origins in juvenile society. The dewlap might have tactile and thermoregulatory functions but the continuous enlargement of its silhouette with age suggests that, for the bulls at least, it is a device to increase the impression of size in neck and shoulders and the differential colouring of the forequarters also serves this end.

The absence of close ties allows eland to vary the size and composition of their associations and Hillman has calculated that all-male groups average three, female groups 11 and juveniles 35. Bulls associate with females or nursery herds for variable periods of time but they are highly independent and are the only class ever seen on their own. Some individuals wander very widely but on the whole Hillman (1976) found the Nairobi Park males were more sedentary than the rest. The strong attachment of some mature males to a particular area and the more limited range of their movements

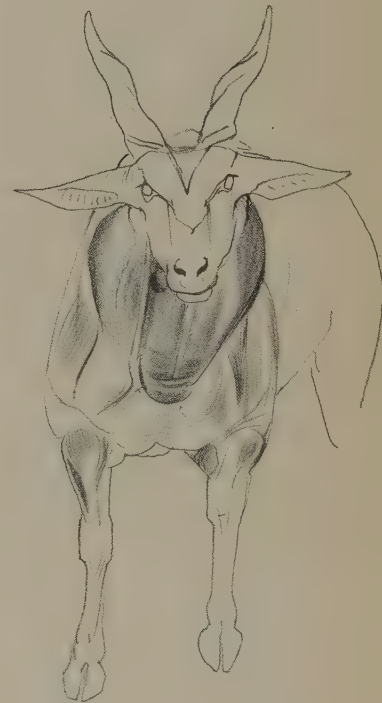


ensures that neighbouring males are frequently in one another's company whereas the females, wandering over areas of at least 200 sq. km, come into contact with many more females and show less consistency in their associations.

Male animals that left the park at the same time as the females were seen to return some five months earlier than the females, which suggested that they did not range as far as the females during the wet season. Some of the older males appear to be less nomadic than others. Adult bulls are seldom found in numbers exceeding six or seven, which may be because the relative rank is easily and quickly established in a small group, whereas larger numbers require an extended hierarchy with a greater likelihood of closely matched and therefore intolerant antagonists. On the one occasion I witnessed 13 males together, there were unusually frequent pushing contests and the party soon broke up into at least two discrete groups. Underwood (in lit.) reported that on one occasion he saw a bull dislodge another from a shade tree by threatening it. The subordinate immediately went to a nearby bull and attacked him.

"A series of fights followed, which ended with the six bulls stretched out in a straight line, from most to least dominant. The line was evenly spaced and covered 200 metres. The positions were maintained for two hours as the bulls grazed. The line then collapsed as the animals went to water and it was not reformed."

The cows are also hierarchical (see p. 43) and similar displacements have been observed in all-female herds by Hillman. He also observed an interesting effect during defence. The lowest ranking cow (one with a broken horn) was forced on to the periphery when the herd bunched against a cheetah. Thus might selection operate against animals of lower rank. Fights between



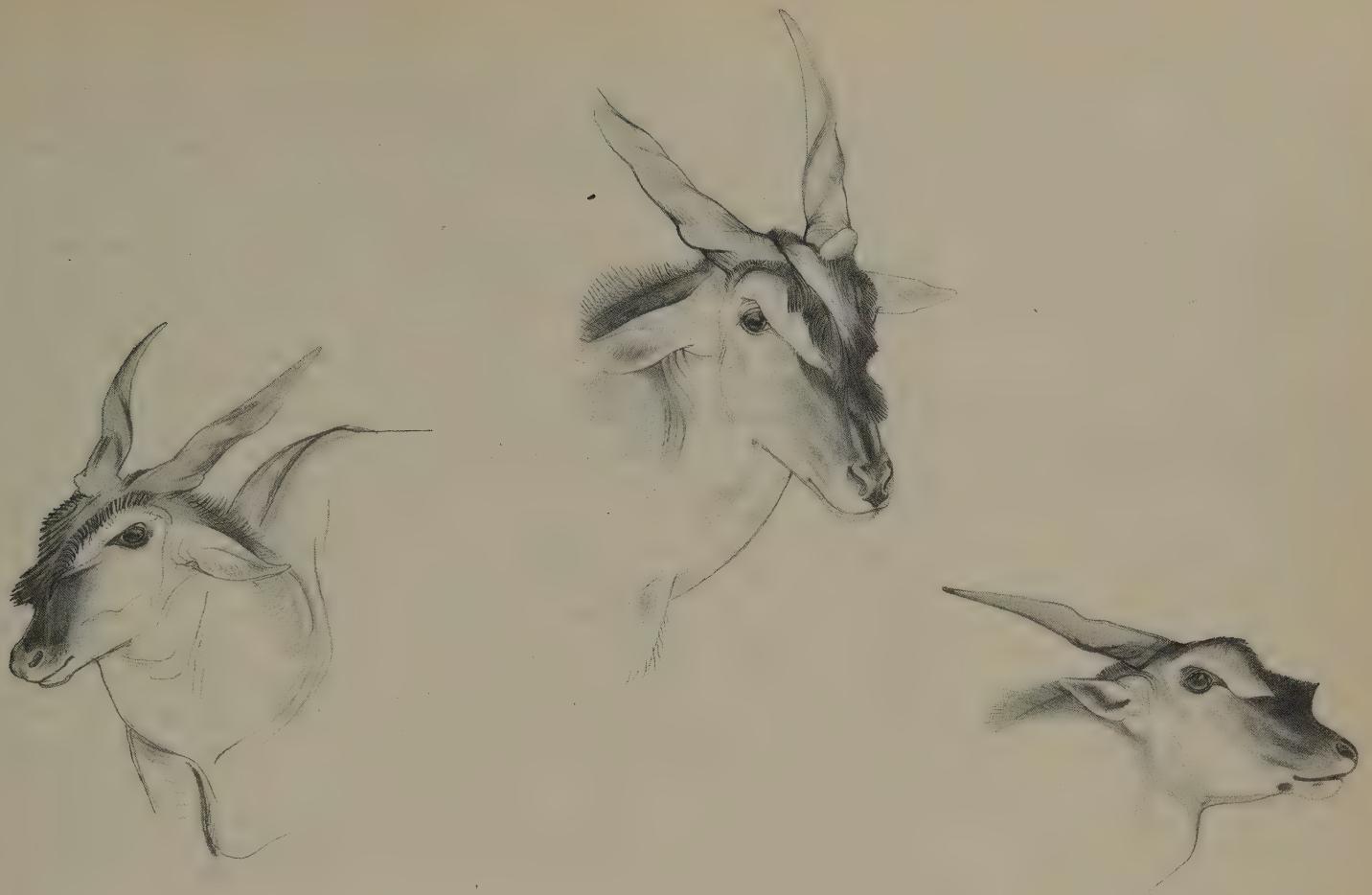
females are rare but violent and the outcome is settled almost immediately.

Actual physical contacts between opposing animals are relatively rare and in any case must occupy only a minute proportion of their time. On the other hand, a visual illusion of superior size probably determines the outcome of many male encounters and may be particularly important when conspecifics make frequent but casual interactions. Broadside display may be incidental to turning round to view a disturbance but the effect is to present a lateral view of the body. It is questionable whether superior size is intimidating or attractive to other eland. Verheyen (1951) thought that a particularly conspicuous old male in the Upemba Park attracted females, but it is unlikely that there were sexual connotations to such behaviour. Young eland tend to gravitate towards larger animals and, in the absence of a near neighbour of their own species, Hillman often saw them approach kongoni. Smaller animals commonly follow larger ones irrespective of their sex and in small groups I have noticed that it is often the largest members that initiate movement. Underwood (in lit.) has confirmed this tendency. As for intimidation, there is no evidence that an animal of larger size repels a smaller one but an approach by the former does seem to elicit a display which may employ both visual and olfactory cues.

If a bull of inferior size is approached, it shakes its head from side to side with a rhythmic rolling movement and evades contact by walking away with neck lowered. This ritualized flagging of the head is matched by a dominant male which, instead, elevates its head and chin, making side-to-side movements, which Underwood (1975) sees as deriving from a chin-pressing movement directed at a subdominant animal's rump. This gesture is seen not only in courtship but also in the mock mountings that are common in subadult and female groups. Underwood suggests it implies dominance. Moss (1975) on the other hand, has reported a tendency for subdominant males to mount dominant males. The heads of both dominant and subdominant animals are only shaken at close quarters and it seems to me very likely that this is not only a visual signal but might serve as an olfactory advertisement of the animal's condition. Furthermore, it may help to explain the function of the thick brush of hair on the bull's forehead.

Rubbing the head is a sign of excitement and both sexes tend to thresh their foreheads about in muddy puddles after a storm. Various scents stimulate the male and Hillman saw one rub its head in elephant's urine and on charcoal. However, the principal stimulus for a bull is his own urine. The freshly wetted soil is scooped through the brush almost every time a bull urinates and the hairs often become thickly clotted with powerfully scented mud, which on drying may puff out in a little cloud of dust when the animal shakes its head. The bull will also rub his tuft in the urine of an oestrous female and this distinction is interesting because female eland, which have no tufts, frequently soak their foreheads in one another's urine but do not do this to a companion if she is in oestrus.


Underwood (1975) has suggested that the frontal skin may secrete scent and that glandular activity might help to induce periodic head rubbing. If this is correct, the observation of females rubbing their heads at about the time of parturition might be symptomatic of a mechanism to acquaint calves with their mothers' odour.



I suspect that, among males, the scent of the brush serves to advertise the owner's condition and that this is directed at other males. On the other hand, when the male impregnates his brush with an oestrous cow's urine, the action is directed at her and might serve to lessen the intimidating connotations of his own scent and thus reassure her; it may even assist temporary bonding. The mutual urine soaking of adult females may be a similar device for overcoming the strangeness of another animal. A general exchange of scent familiarizes all group members with one another and in a nomadic and open society this may be an important factor in generating a sense of security and cohesion within the group.

Like most male antelopes, a bull eland horns the ground, vegetation and other landmarks and this is probably the derivation of the motor pattern in tuft rubbing. When a male saturates his forehead with an oestrous female's urine this can be seen as an extension of olfactory sampling and similar behaviour may also explain the female's urine marking but it does not explain why a bull's own urine should be a specific stimulus in this respect. It was mentioned earlier that the length and colour of the frontal brushes wax and wane. If the female also shows periods of increased head-rubbing, there is the possibility that these are the signs of subtle biochemical cycles. It would be most interesting to attempt a correlation between all types of glandular activity and the major events in an eland's life cycle.





Hoof, foreleg and tail flashes form two tiers of dark marking; the back-line a third.

In spite of the fact that membership is freely exchanged when female groups converge, they are strictly cohesive while on their own and it is rare to see a solitary female. Indeed I have observed that the members of a group temporarily dispersed by my Land-Rover were restless and reluctant to move until they were all reunited. Sight, smell and sound are commonly employed in the process of re-grouping. Individuals parted by thick bush use their voices and observers have remarked on the eland's tendency to call in a strong wind, which could be a compensation for diminished olfactory communication. Underwood (1975) has detected scent in the region of the false hoof and suggested that this might create scent trails.

The contact bleat is made by all classes and the juveniles' want-call apparently carries well as animals respond over distances in the region of half a kilometre. It is heard in captives awaiting their keeper by the food stall and in a male approaching the female. Like other tragelaphines, both sexes can utter a loud bark when alarmed, and fighting males grunt and snort. Some eland make a clicking noise, which is often described as emanating from the hooves but is in fact made by the sinews of the knees. Hillman (1974) has determined that this is a peculiarity of the older males and is made by the joints of the forelimbs only. If weight plays the key role I have suggested, it is possible that the click might communicate information on the status of a bull as the sound could be correlated with the weight-load. Hillman saw a young bull suddenly cease its attentions to a cow and drop its head to the grazing position before an approaching old bull was in sight. The animal was apparently responding to the sound of the old bull's clicking sinews.

It has been noticed that captive bull eland, like other tragelaphines, have periods of *ukali* (p. 102), when normally placid males become intensely aggressive and are very dangerous to other males and also to their human keepers. Indeed, a keeper in Woburn Abbey was killed by an eland in this condition. *Ukali* can last for a few days or even months but it is said to average about three weeks (Fox, personal communication). It is of irregular appearance in captivity but if it occurs in the wild it might have some synchrony with mating peaks. However, it should be stressed that this phenomenon has no direct relationship with fertility and the male eland's sexual physiology shows no changes throughout the year (Skinner and Van Zyl, 1969), which is consistent with my interpretation that *ukali* might represent a dispersal mechanism for males that is independent of sexual behaviour (see pp. 49, 149). Horning of the ground and bushes is frequent, particularly if another male is in sight, in which case a *kali* bull may circle around in a very slow walk with the proud stance, tilted head and rolling eyeballs, while the hair of the neck and frontal tuft appear to be more erect. Fox (personal communication) described seeing such a bull deliberately using a female as a "stalking horse" to launch a surprise attack on another male.

Eland bulls are typical tragelaphines in a general avoidance of confrontations. While a lesser bull usually gives way to the larger bull it is possible that *ukali* might sometimes determine relationships where size differences are relatively ambiguous. Since its manifestations are inconspicuous, avoidance behaviour by other elands might mask the presence

of *ukali* from an observer in the field and there is no confirmation of its existence in wild eland. Hillman only saw two fights, both of which were abrupt charges over a short distance and both involved competition over a female.

Fights start with a short rush and, with chins tucked into chests, the opponents engage the tips of their horns; throwing their weight into the clash they twist and stab to try to gain advantage. One or both opponents may drop on their knees, which puts their weight more directly behind the lowered head and makes their stance more stable but limits agility. Fighting is generally attributed to direct competition for oestrous females but Verheyen (1951) commented on the lack of interference between neighbouring males even during the Upemba mating peak. Underwood (1975) has described inter-male competition as being very variable but he commented (in lit.) that rising aggression in any one bull might be reinforced by an increase in the frequency and intensity of aggressive responses in other bulls. From my own observations of a *ukali* captive it is clear that any threat by a human, even staring at an animal, elicits a storm of charges and horning, whereas discreet evasion, preferably with averted eyes, has an appeasing effect. Females may also exhibit fits of aggressive behaviour, at which time captives have been seen to keep other animals away from troughs for a day or two.

Courtship involves persistent following and circling by the male, which makes conspicuous motions of licking and tries to rest his chin on the oestrous cow's rump. The dewlap tends to come into direct contact with the root of the tail or even the vulva, so it is possible that the dewlap has tactile importance.

The congregation of groups in open country sometimes appears to coincide with both birth and mating peaks. Gestation is from 260–284 days and a post partum oestrus of up to 30 days ensures that some females conceive soon after birth, giving an average calving interval of about ten months and a very irregular timing to births. Hillman has reported a captive cow bearing eight calves in six years. Skinner and Van Zyl (1969) recorded birth intervals in two distinct habitats and estimated that those living in the high veldt produced calves somewhat less frequently than those in the bush veldt. An overall average of 83% of the females calved each year. Notwithstanding these differences, the majority of births in southern Africa are between May and November with peak numbers in July–September. North of the equator, in Karamoja, there is evidence of considerable differences from year to year and perhaps from population to population. In 1955, calves were recorded in the Kidepo area during January, February and March, while elands in central Karamoja concentrated in one particular valley, where they dropped 96 calves during the month of June (U.G.R., 1955). In 1963, elands gave birth in this area between October and December and in the following year there were numerous births in September. Elsewhere in East Africa there might be some correlation between the concentration of animals during the rains and sexual activity. Hillman (1976) has recorded births throughout the year but he also found that the timing of peaks tended to vary from year to year.

A calf is able to walk almost immediately after birth, but remains concealed for about two weeks, after which it joins the mother in a nursery group. During the period of concealment, the mother visits it twice a day and the calf sucks for about three minutes, following which it is very active and playful for a period of time that increases each day. After a last token suck it returns to its hiding place and remains immobile until its next feed.

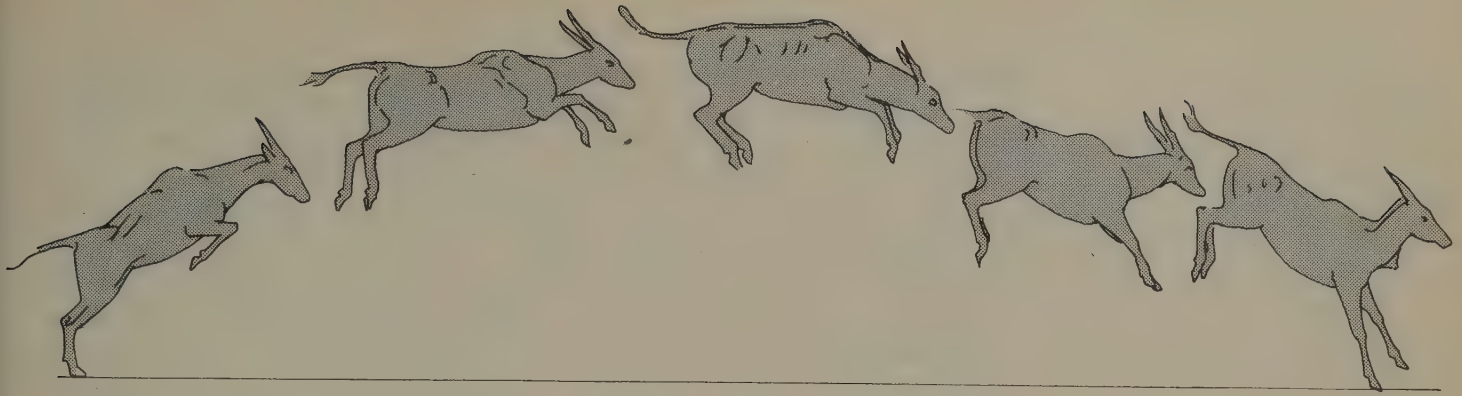
A calf weighs 22—36 kg at birth and grows extremely rapidly; a male can weigh 466 kg at the age of one year. Horns also grow very fast; they are rather soft up to the age of six months and are easily distorted. The shafts of the horns tend to be mostly parallel in females and may be more divergent in males but there is considerable variation in the angle, length, thickness and twist of horns. Hillman (1976) has recognized some ten relative age classes in the male based on coat colour, horn development and the size of the dewlap.



Development of forequarters and dewlap in ontogeny of male. Emphasis away from hairy tassels and height towards *mass* of forequarters.

Mortality is high in young elands, with predators, disease and accidents all taking their toll. It is possible that an equal sex ratio at birth changes in favour of the females. Estimates of adult males in the population vary from 14% to 25%. The differences may be due to the greater conspicuousness of the gregarious females as well as to real variation in different regions.

Some measure of the relative importance of predators in the Kruger Park is revealed in Pienaar's (1969a) records of kills—65 by lions, nine by leopards, three by wild dogs and one by a cheetah. On the other hand, adult



eland were killed less frequently than numerical abundance would warrant, which is some indication of the effectiveness of their defences. In East Africa, hyaenas are sometimes an important predator. Slow and solitary old males would be vulnerable to large groups of lions but, because the larger prides prey mainly on herds of plains ungulates, they seldom hunt in the more thickly wooded country that is preferred by old bulls. Bunching and aggressive defence by the females has been seen against all their major predators.

On one occasion Hillman saw a lioness stalking a kongoni by moonlight and using cloud shadows to advance. The kongoni escaped and the lioness' charge took her up to a group of female eland and their young that were standing beyond. The young grouped behind the shield of their mothers (as they do for wild dogs, cheetah and hyaenas) and the females then advanced and chased the lioness off at the run. They are very often in the company of zebras and joint defence has been seen on more than one occasion. In Uganda, a single zebra stallion was seen to rush at wild dogs circling a mixed bunch of eland and Kruuk (1972) has seen female eland that were walking with zebras attack hyaenas that attempted to hunt their companions. He also saw females come forward to attack a pack of hyaenas that chased an isolated calf. This calf had originally stayed close to a bull grazing nearby but had been ignored and even butted by the bull, in spite of the calf's having been bitten and severely harassed by two hyaenas. Females, too, may on occasion be quite indifferent to the fate of their young, particularly when they are strung out in single file, when a predator may take the hindmost, which is often a calf.

As the calf grows older, it develops an exaggerated propensity for flight. Hunters attempting to stalk a herd always try to avoid alerting young females and ranchers have also complained at the frequency with which animals in their second year try to escape and when they are successful they may travel considerable distances. Hillman has remarked (in lit.) that the failure of older animals to follow a spooking juvenile generally results in its circling and returning and as it gets older it takes to flight less readily. Once this phase is over, captives become placid and manageable again and the tendency to disperse may be tempered by a definite attachment to place. For example, a female that was reared and kept with domestic cows returned to her Moroto paddock each of three times the herd was rustled.

Hillman (1974) has determined that females and their young in the Nairobi-Athi area cover a total range of some 1,500 sq. km in the course of a year; the males however, range over only 25—100 sq. km. With such

movement one can seldom expect estimates of density to encompass the total range of a regional population. In the Tsavo region, which probably embraces the ranges of most of the eland found there, the animals are generally dispersed but density increases in the south-west. In this area of 42,500 sq. km and uneven population densities Cobb (1976) counted a total year-long population of 6,750; this is a much lower density than that suggested by the Shinyanga game destruction experiment in which 891 eland were shot in an area of 1,500 sq. km but there was evidence that this included a concentration zone for a larger area (Potts and Jackson, 1952). In the Ankole-Masaka tse-tse clearance scheme 646 eland were killed in an area of 3,000 sq. km.

The eland's continuous movement over a vast range, its low density of numbers and small well dispersed groups, its need for shade and rest in the dry season and its inability to survive on coarse grazing create very real problems for the management of this species in the future. Huygelen (1955), Hirst (1961), Cmelic (1964), Robson (1964), Skinner (1966, 1967), Retief (1971), Lewis (1975) and others have discussed the domestication of the eland and there have been sporadic attempts at breeding and ranching for over a century in such diverse countries as Russia, Britain, North America, France and Brazil.

Game animals are not accepted by farmers unless they can fit into some established management system and their productivity has been proven over long periods. Ranches that are big enough to contain economic herds have to contend with predators for which tame or semi-tame eland are easy prey, and Lewis (1975) has shown conclusively that eland are not suited to being coralled at night and herded by day. Attempts at farming these animals in settled areas are expensive, for unless the animals are fed concentrates they lose condition or degrade the range and if they are not herded in very small units or confined by fences 3 m high they will wander. Unless they are conspicuously marked they will fare no better than a wild nomad on entering other farms.

In regions with a hot dry season, herding the animals by day and confining them by night deprives them of the long midday rest that is a physiological necessity. It is significant that the eland studied by Lewis, which were coralled and herded like local cattle, rested and ruminated for only 12% of the day, whereas wild ones may spend up to 50% of the day resting. These domestic eland were feeding for 70% and walking for 14% of the day, so that their artificially induced activity exposed them to heavy heat loads and a predictable rise in energy requirements. This in turn probably demanded more time for feeding. However, wild eland also spend a long time eating because their mouths and teeth are adapted to gathering scattered plants by small carefully selected mouthfuls. With all these practical disadvantages many former enthusiasts for the exploitation of the eland have lost interest, yet the animal has physiological and ecological adaptations that may yet prove extremely useful in diversifying man's exploitation of certain kinds of habitats as well as providing special diets for invalids or for the fortunate.

Eland cows yield a gallon of milk a day (11% fat, 8.9% protein) which can stay fresh for days. It is said to be exceptionally digestible. The butter

has a high melting point, the meat is tasty and is the product of an exceptional growth rate. Skinner and Van Zyl (1969) have demonstrated how nutrition and habitat alter growth rates and Stainthorpe (1972) recorded eland heifers giving birth at the age of two years when fed concentrates as against three years when not. The most sustained effort in the domestication of eland has been in southern Russia, where a herd has been maintained for over 70 years (Treus and Kravchenko, 1968). The eland could therefore be a candidate for intensive management as high grade stock but this would require acceptance of capital costs on a similar scale to those invested in pedigree livestock and a more general recognition of the excellence of its meat.

In the drier wooded grasslands, which are of marginal value to agriculture, water and the tse-tse fly delimit the distribution or numbers of livestock over large areas. Where these natural controls do not operate there is often evidence of progressive degradation through overstocking. Blankenship and Field (1972) have found that eland move out of range that has deteriorated through overgrazing by domestic stock and this has undoubtedly been a factor influencing the patchy distribution of the species today. However, free ranging eland are not incompatible with cattle and they are hunted or cropped in small numbers on several well-managed ranches. Eland are susceptible to rinderpest and malignant catarrh and other cattle ailments but are resistant to trypanosomiasis and East Coast fever. While its specialized adaptations preclude the eland's replacing or even competing with cattle in terms of general productivity it can often contribute to the diversification, amenities and profitability of ranching.

In the prehistoric paintings of Kondoa and in the rock art of southern Africa, the eland is the most frequently represented of animals, which is perhaps more a measure of the bushmen's preoccupation with the animal than an indication of its abundance. As with the horses, cattle and bison represented in European cave paintings, still lives of seventeenth century Holland and advertisements in the modern world, beauty lies not in the eye but in the stomach of the beholder.



Bongo
(*Boocercus*
***eurycerus*)**

Family

Bovidae

Order

Artiodactyla

Local names

Solugot (Sebei), Sirogoyta (Kipsigi),
Siribeyi (Marakwet), Ndongoro (Kikuyu).

Measurements
head and body

220—235 cm

height

122—128 cm

tail

24—26 cm

weight

300 (240—405) kg males

240 (210—253) kg females

horns

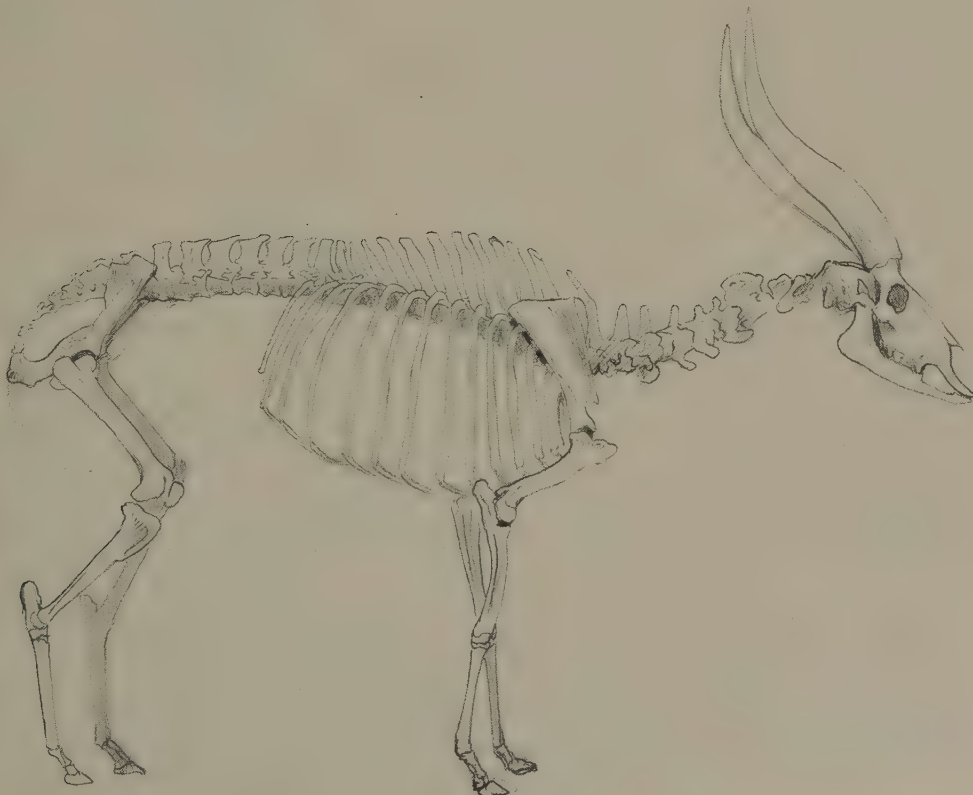
60—100 cm

Bongo

(*Boocercus eurycerus*)

In common with other tragelaphine antelopes the bongo is spiral-horned, flat-sided, has a dorsal crest, stripes (numbering 10 to 16 on each side) and black and white markings on the extremities. On the forequarters and limbs of males the red darkens and finally turns black with age. Weight also continues to increase slowly and an old bull is reminiscent of a slab-sided painted ox. However, body size and limb proportions vary greatly, some individuals being tall and others short. In addition to differences between individuals there are those between regions, with Kenya bongo consistently heavier and taller than those from West Africa.

Females are predominantly red and white, old cows are sometimes paler but only slightly larger than other adults: their horns are more slender than those of males; their enormous ears are particularly flamboyant. In a dense habitat large ears must improve hearing but in an animal that apparently relies on scent less than do other antelopes, the black and white marking of the ear enhances their use as intraspecific signals. The greater intensity of colour and tonal contrast in bongo markings is probably related to their being relatively "visual" but also predominantly nocturnal animals and to sharply fragmented or poor illumination in their habitat.





Total range of *Boocercus*

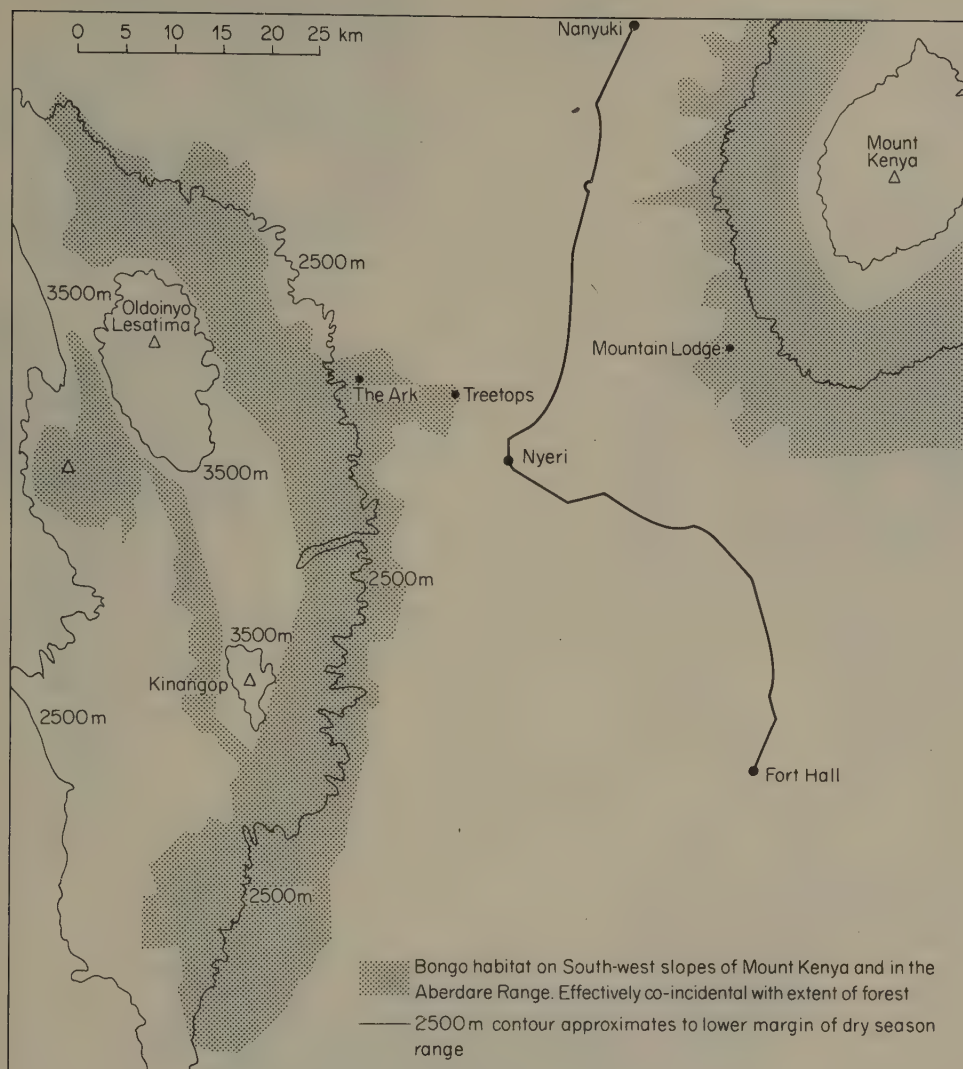
Like the eland, bongo range very widely in their quest for the high-concentrate green herbage on which they are dependent. However, they are shorter-legged, slower and shorter-winded than the eland. Being vulnerable to large predators, their lack of stamina prohibits them from moving very far out of dense cover where they can hide or protect themselves.

Being large and relatively social animals the nutritional needs of a viable population can only be met in areas with an abundant year-long growth of herbs and low shrubs. The normal vegetation climax under high rainfall regimes is forest which soon shades out low-level herbage. The latter can grow along margins and in glades created by fallen trees but only becomes extensive in areas where shade has been suppressed on a larger scale. Landslides, floods, communal die-offs, elephant herds, human cultivators and foresters all leave conditions behind them that suit an ephemeral regeneration of low herbage. Regular browsing by large numbers of elephants can help maintain extensive areas of low thicket. The gregarious dying off of extensive stands of bamboo also creates pastures of herbs, shrubs and creepers. A close examination of the few areas where bongo flourish reveals in every case a fragmented mosaic of pasture, forest and thicket and the scattered distribution of bongo populations is some testimony to the rarity of suitable habitats.

In the Azande region of the southern Sudan there has been sporadic cultivation and seasonal firing in an area laced by very numerous gallery forests. During the protracted civil war of the 1960s large stretches of country ran to fallow, and the ecological conditions that have ensued have suited the bongo so well that the species is now abundant. The Azande have also selectively hunted the bongo's predators and competitors while leaving alone the bongo, which is locally taboo. Today the area is a major stronghold of the species, very largely because of this unique combination of circumstances. However, as human populations are returning to the area and increasing again, ecological and cultural conditions are beginning to change and a future decline in the Sudan bongo population can be predicted.

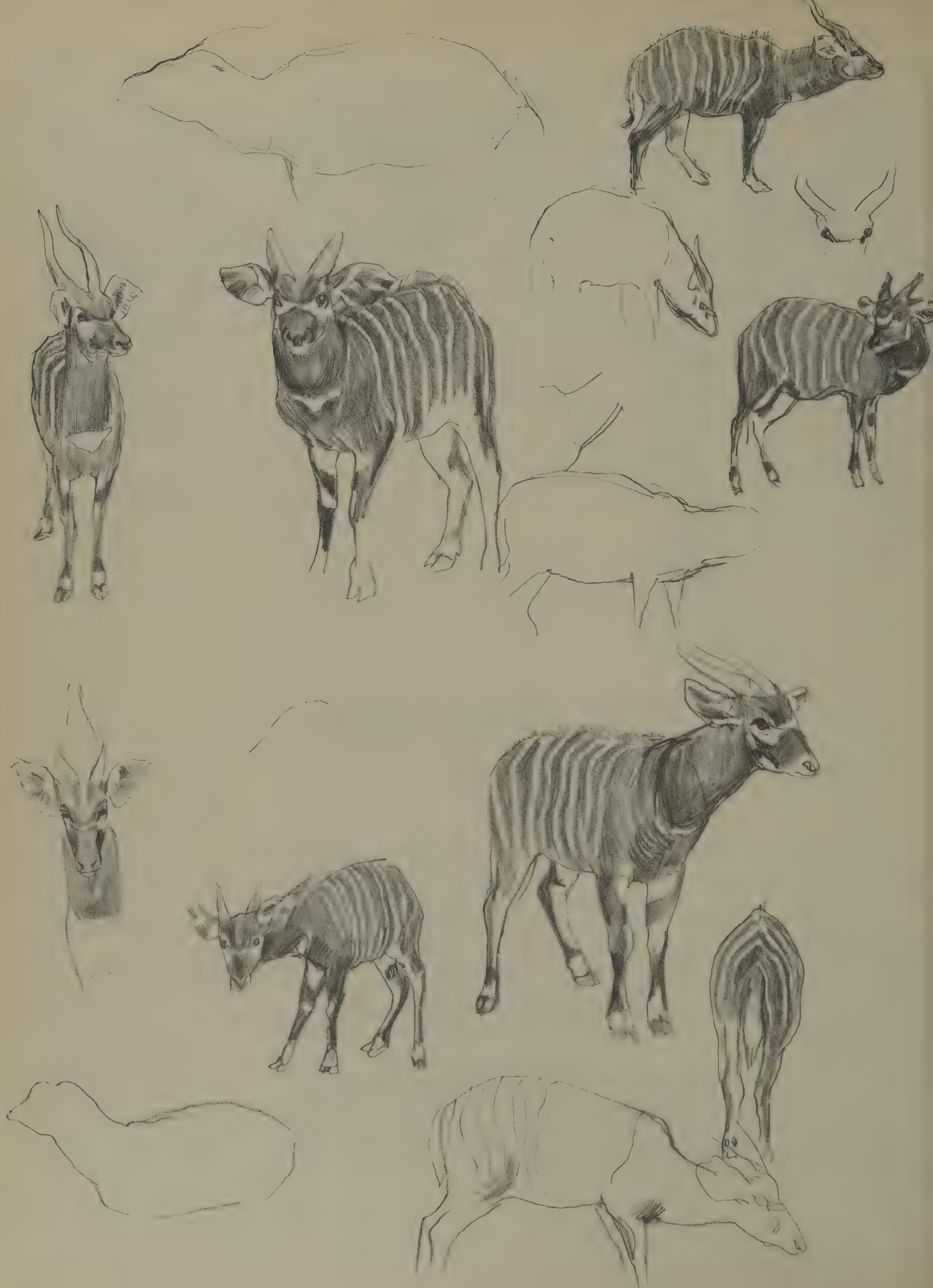
Within the main block of lowland forest, bongo tend to occur in areas of shifting cultivation, logging, or elephant concentration. For example, I found numerous bongo tracks in an area of the Tai National Park in Ivory Coast where pirate logging companies had opened the forest and elephants were maintaining "elephant tangles" or low thickets; grassy glades were heavily grazed by buffalo and giant hog.

The best known area of their range is central Kenya, where a population, currently estimated to be well in excess of 500, lives in the Aberdare Mountains. Here the bongos follow a seasonal cycle, with the moist upper rain forest and bamboo zones providing dry season pasture, while secondary growth over ancient cultivation sites on the lower reaches of the mountain allows a wet season dispersal. In February and March, when the animals tend to be concentrated at high levels, Edmond Blanc (1960) found *Paro-chetus communis* and *Senecio biafrae* to be preferred foods on Mt Kenya. Root (personal communication) has noted *Impatiens* spp. (Balsam) and a variety of creepers to be their main food on the Aberdares. He found that bamboo shoots were eaten by captives but were less frequently eaten in the wild. *Sericostachys scandens*, *Rubus*, *Asplenium*, *Ranunculus* and *Mimulopsis* spp.



are dominant at higher altitudes and are probably all major food plants. The last species flowers communally at irregular intervals of three to ten years, and Simon (1962) saw several dead bongos and also evidence of heavy scouring during the second year of the *Mimulopsis* growth cycle. The local Wanderobo hunters, who first brought Simon's attention to the phenomenon have long recognized that *Mimulopsis* at this stage of growth poisons not only bongo but also forest hog and cattle. (I was told by an Nderobo hunter that a very virulent human hay fever is associated with the flowering.) Laboratory tests have confirmed that extracts from second year *Mimulopsis* stems are poisonous.

The evidence suggests that mortality might be quite heavy in some localities; the animal itself does not seem to recognize the biochemical change in its accustomed food and it is, in any case, a dominant plant throughout the bamboo zone. Implications for the conservation of the species could be important and the phenomenon deserves further study.



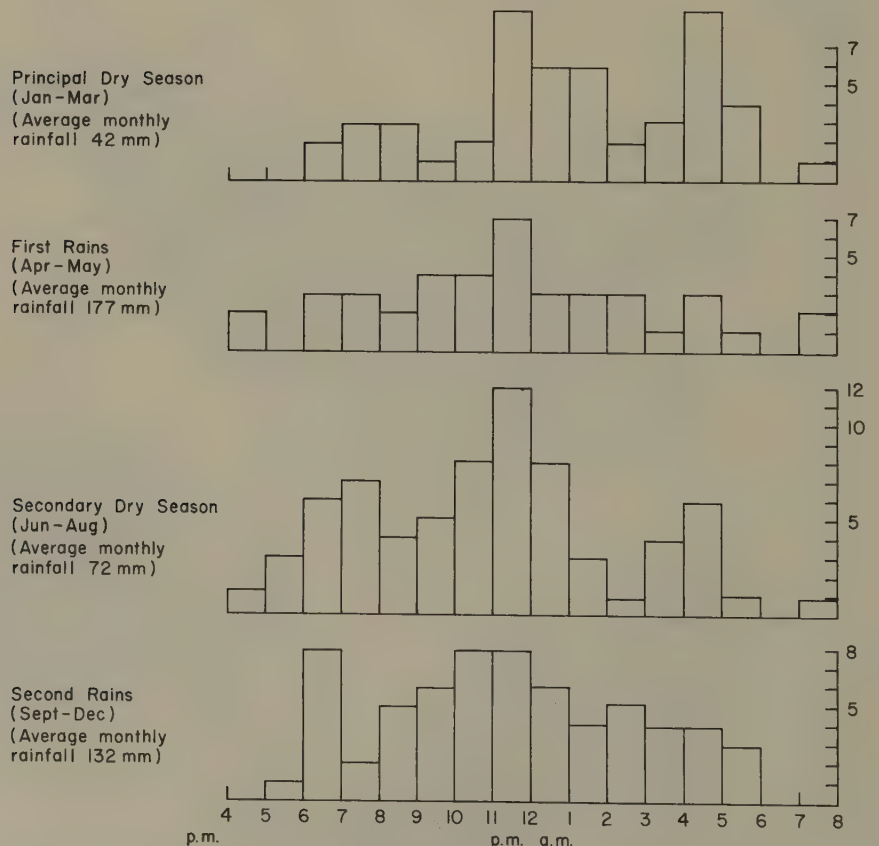


Creepers are the one type of high-level foliage that bongo can exploit. When numbers of animals are engaged in pulling these plants down from the canopy above they can generate considerable noise (Hillman, personal communication).

At lower levels of the Aberdares some of the dominant shrubs may provide some browse, notably *Cassia didymobotrya*, *Vernonia auriculifera* and *Crotalaria agatiflora* but it is probably relatively short-lived herbs and some young grasses that provide the bulk of their forage.

Occasionally bongo will enter marshy or boggy areas, and Prickett (personal communication) has seen a solitary bull feeding on water plants. The occasion was very unusual for being at noon but it was a cold and misty day in the wet season.

Ionides (1965) found that they tend to avoid movement and shelter under dense forest during heavy rain but feed intensively once the rain has stopped. They normally lie up in thickets and ruminate between about 10.30 and 4 p.m. I have been indebted to the Park Warden and rangers for the opportunity to watch bongo in the Park, and to the Directors and Staff of the "Ark" (a viewing lodge built over the Yathabara glade) for detailed records of sightings, and particularly to R. J. Prickett and S. Waller for many interesting observations.



Timing of visits and numbers of bongo groups visiting Yathabara glade in 1975. Seasonality for the year indicated by average monthly rainfall for each season.

Records of bongo visits to the salt-lick at Yathabara give some indication

of their activity cycle with the first animals generally coming in after 4 p.m. Peak activity is between 11 and 12 p.m. after which there tends to be a lull which probably represents the nocturnal rumination period that has been observed in captives (Root, personal communication). Further activity occurs between 4 a.m. and 5 a.m. This pattern is most in evidence during the drier months following the heavy rains. It also appears in the main dry season, except that animals do not come into the glade before dusk and prefer the hours after 10 p.m. During the rains activity is more continuous (see diagram opposite).

The composition and number of groups visiting Yathabara glade varies seasonally, partly because of the annual movement up and down the mountain and the strategic position of Yathabara on the eastern salient. Although records of individuals have not been kept, some animals have distinctive stripe, colour or horn-patterns and it is known that particular adults only pass through once or twice a year, others are seen infrequently and a few are relatively regular visitors. Males are more easily recognized as individuals and once in a while a bull visits that has never been seen before (Prickett, personal communication). This pattern of sighting suggests that bongo wander very widely over the Aberdares and that all ranges probably embrace both high and low-lying pastures on the mountain. However, most animals probably tend to range over a relatively restricted sector of the mountain. The extent of male, female or subadult ranges is not known but probably varies between about 120—300 sq. km, with occasional males wandering over even larger areas. Most of the male population is solitary and adult males, particularly those of similar size or age actively avoid one another, but old bulls are sometimes accompanied by much younger bulls. Bulls have been seen to spar with their horns in the leisurely rather ritualized fashion of other tragelaphines but this is a rare occurrence. A fight below one of the mountain lodges, Treetops, resulted in one animal dying of a pierced lung. A captive bull, which was wild-caught as an adult and eventually died, was found to have old horn wounds in its chest and shoulders and broken ribs, all of which had healed. Other animals with healed fractures of the legs and ancient snarewounds suggested that lying up in secure retreats can allow maimed animals to recover.

Visual displays are likely to play an important role in intimidation and an aggressive male bulges the neck, rolls the eyes, holds the horns vertical and paces slowly and deliberately in lateral position. However, males do not appear to converge in numbers for display ceremonies such as those performed by bushbuck nor are there hierarchically organized bachelor parties like those of the eland. Bulls sometimes horn the ground and surrounding vegetation and bongo "wallows" probably describe the resting places of bulls that have demolished all vegetation within a radius of about two metres. They do not normally wallow in mud holes as buffalo do. Examining the resting places of male bongo immediately after disturbing them, Sutton (personal communication) noticed a blood-like liquid on the ground. Rain running through the coat would appear to acquire this peculiar colour and consistency.

Males do not herd females or coerce them, nor do they influence the number of cows in a group or their movements. The scattered distribution

of animals puts a high premium on seeking out and testing cows rather than on direct competition for isolated copulations. Although a male's interest in a group of females may be relatively short-term there is evidence that one bull may harass, threaten or simply tail another that is escorting cows. Prickett (personal communication) has described an old bull, hunched and thin, accompanying seven cows. Immediately after this group left the salt lick, a larger but younger bull strutted into the glade slowly following in the footsteps of the others.

What clues do the bongos use when following one another? Hearing may be adequate in some circumstances but only scent is suited to long-distance tracking. Yet bongo are unique among tragelaphines in lacking inguinal glands, nor indeed do they give evidence of any other localized glandular secretions, so dung, urine and perhaps a more general body odour seem to be the most likely clues.

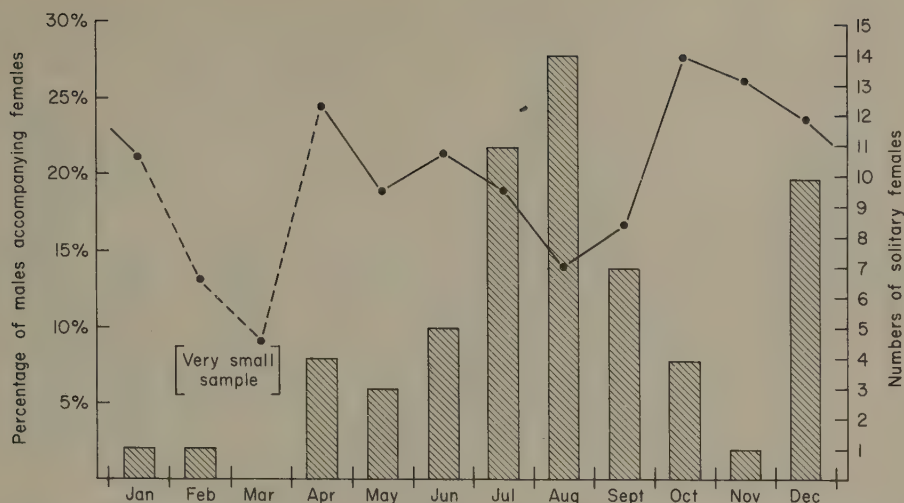
Their vocal repertory, while very limited, resembles that of the eland; the males grunt and snort, the females have a weak, mooing contact call with the young and all classes bleat in distress. Hunters have reported hearing a hissing whistle which may be a contact call or perhaps an alarm. I have found that bongo tend to wait until they can see an intruder, keeping still until the last moment before breaking cover. They run with the head held low and the horns lying along the neck and shoulders; there are often hairless patches where the horn-tips touch the shoulders.

Only females and mobile young are social but there are seasonal changes in group members. Cows are thought to use preferred calving grounds, which are relatively restricted in area and to some extent "traditional" (Wambui, personal communication). There may be associations between cows calving in the same locality and between cows and their female offspring. Although female groups tend to form and dissolve readily there are signs of their hierarchic relationships, evident in horn tilts and threats with cows tending to defer to larger, and longer-horned individuals.

Such herds are often strung out behind an old cow in the van. This leader will often remain quite still in cover before coming out into the open. Prickett (personal communication) has sometimes seen a cow walk out and inspect the Yathabara salt-lick after which she returns briefly into the bushes, then to emerge with other cows or calves.

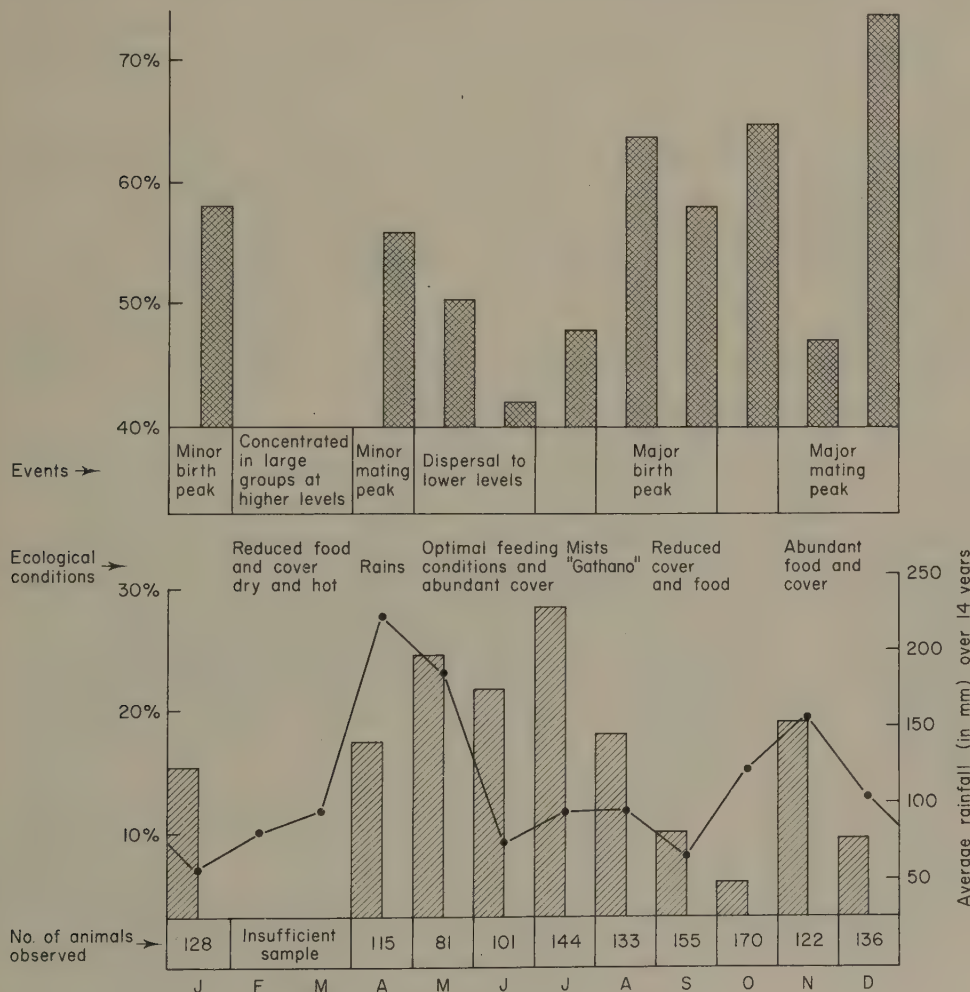
If interrupted at the lick (especially by buffalo) they may move into nearby cover and then stand quite still with their backs to the disturbance; periodically an animal turns its head but the bongo only turn round and come back once the intruders have left. It is possible that the body orientation is significant, as bongo tend to turn round in response to any disturbance. Not only is the hind-view less conspicuous, but they are prepared for flight should the situation warrant it.

Records of bongo visits to Yathabara reveal seasonal changes in group composition and numbers among the female and nursery groups. They confirm that on average more than three-quarters of the male population are solitary, but that they monitor female groups continuously. The presence of oestrous cows clearly increases male interest in these herds and there is a seasonal cycle in the incidence of male attendance (see opposite).



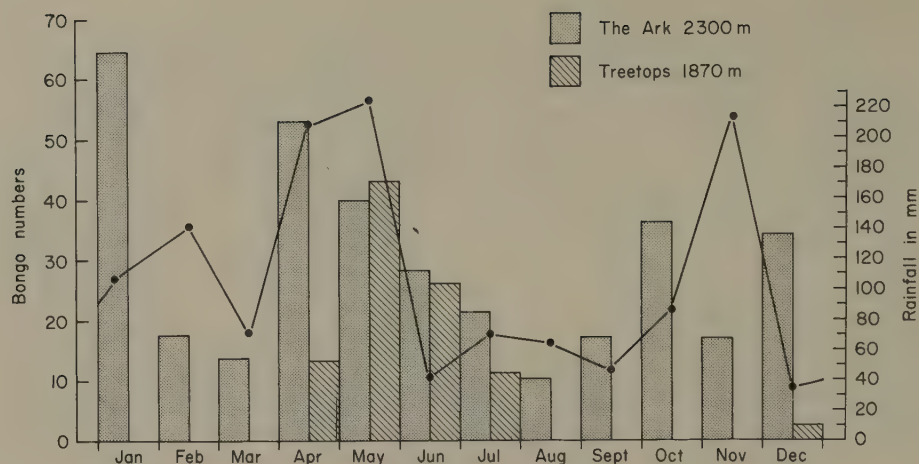
Mating peaks, suggested by percentages of males accompanying females, plotted against numbers of solitary females (histogram) suggestive of birth peaks nine months later. (Oestrus influences the incidence of male attendance on females, while solitary females are almost invariably close to parturition.) Yathabara glade, 1971—1976.

In the Aberdares I found an overall average group size of 2.5 but for 23 groups that contained calves or juveniles the average number of animals was 8.25 (range 3—27). The increase could be attributed to the mothers with calves or juveniles at heel seeking out other females, and three months after the major birth peak in July—September, nearly all females travel in large groups (see above). There can be little doubt that large nursery herds form



Group sizes of adult female bongos visiting Yathabara glade, 1970—1976. Above: percentages of animals in large groups (nine or more). Below: percentages of animals in small groups (two to four). Note that mists ("Gathano") extend a period of precipitation and its effects.

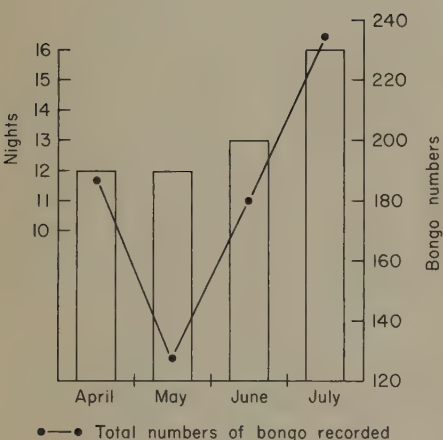
Numbers of bongo recorded at the Ark (2,300 m) and at Treetops (1,870 m) in 1973 with rainfall for the period to illustrate wide dispersal, especially to lower altitudes during and immediately after the long rainy season.



for group security, particularly when there are numerous calves around.

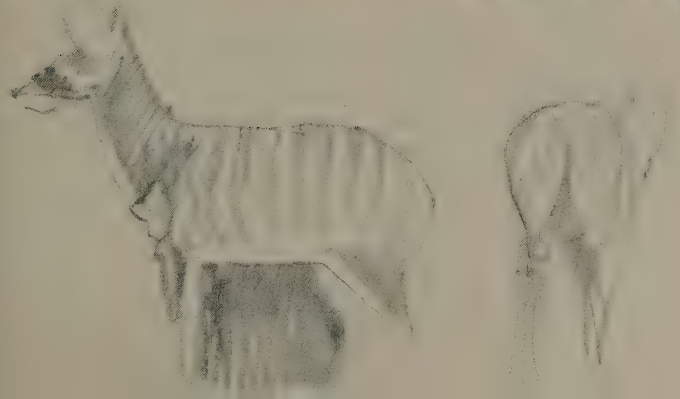
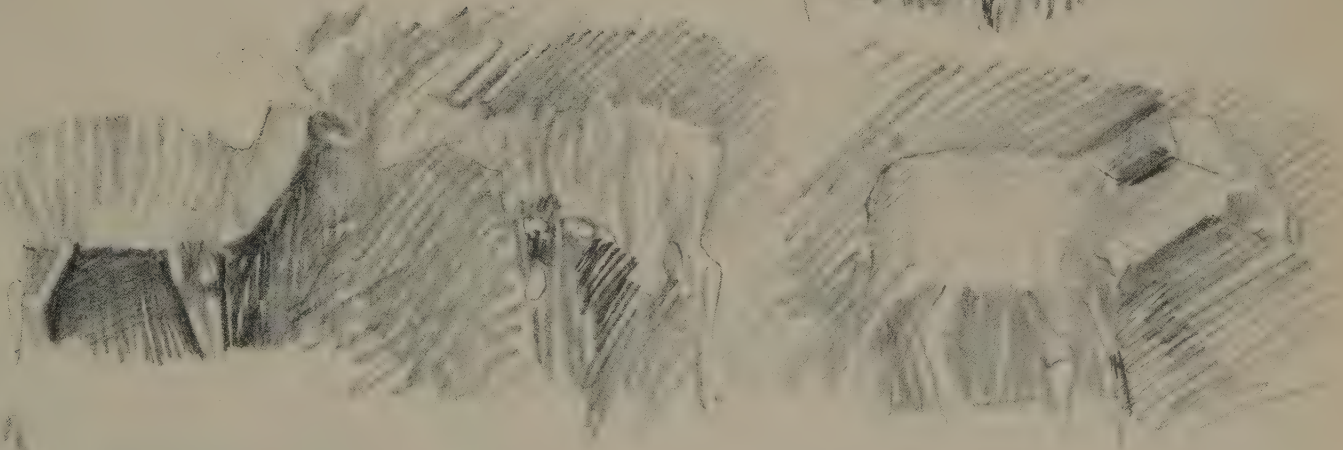
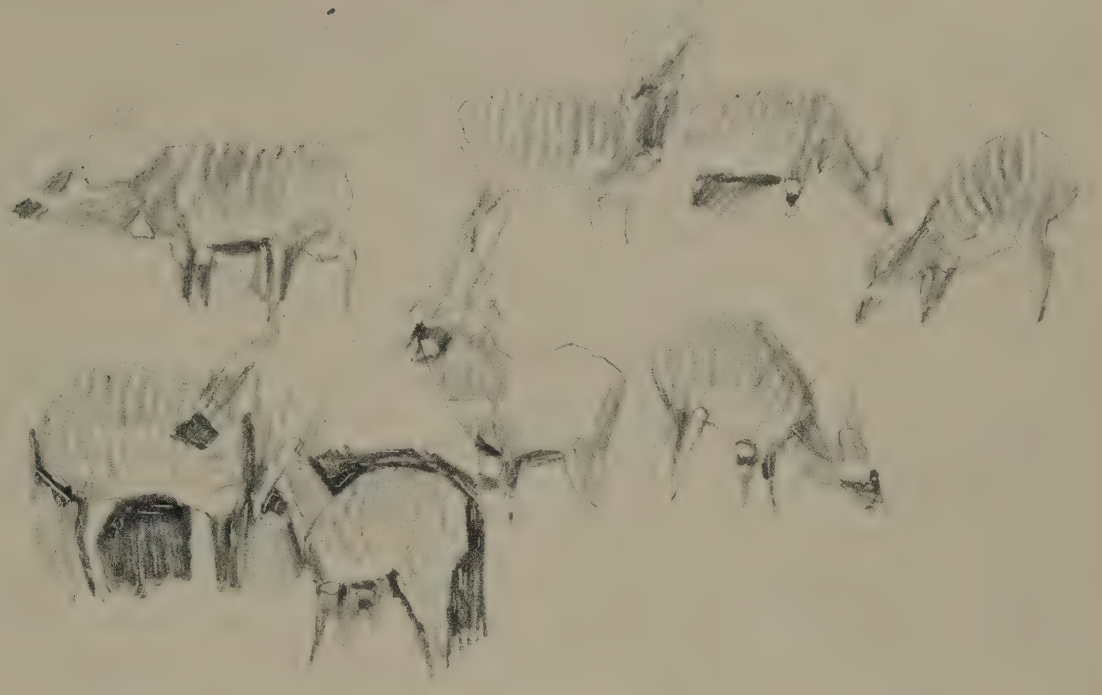
At the end of the dry season bongo congregate at higher levels and animals are recorded less frequently at the viewing lodges further down the mountain (hence lacunae in some of the histograms).

With the arrival of the long wet season, heavy rain, mist and cold drive the bongo down and generally favourable conditions allow the animals to disperse over the lower reaches of the mountain in smaller units (see above). Thick vegetation provides abundant food and increases security from predators. Because it is less necessary to travel in search of food, contacts between groups are probably reduced. Thus bongo move less in May than in other months and their feeding pattern is temporarily similar to that of sitatunga in comparably rich habitats (p. 87). A month or so after the rains are over browse becomes scarcer and the animals begin to move about more, which brings the small units into more frequent contact with one another. In spite of variations from year to year an overall rise in average numbers of animals and an increase in the average frequency of visits to Yathabara glade between May and July reflect an increase in activity over this period (see margin).



Increased activity between May and July implied by greater numbers observed and greater frequency of visits to the Ark, 1972—1976. Histogram: average number of nights with bongo visits.

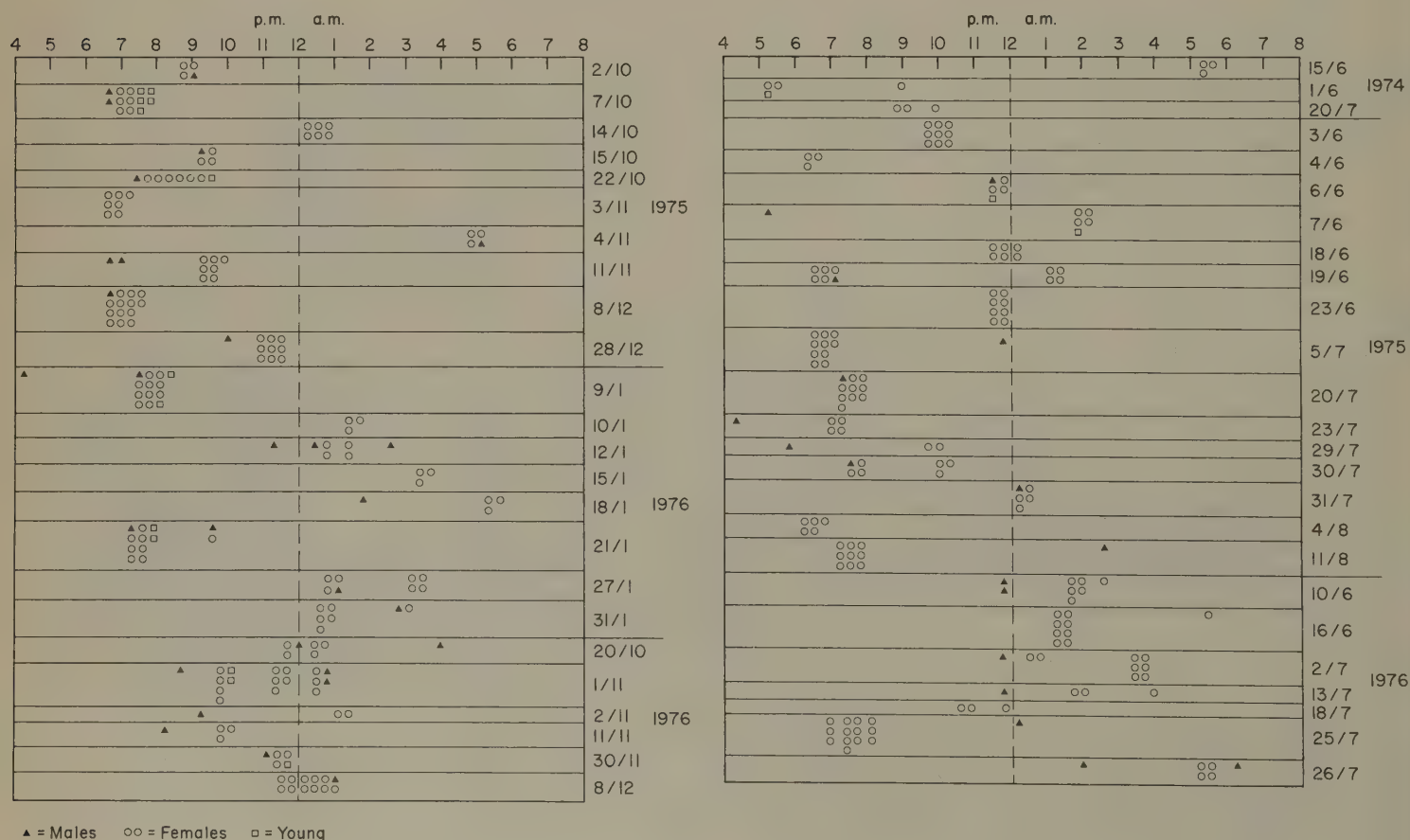
Since drier conditions favour predators, resulting in more harassment, more frequent meetings probably encourage progressive amalgamation of small groups. This process may be given added impetus by another event—the calving season. Because females near to parturition become solitary, it is likely that their deserted offspring and other companions tend to join larger groups at this time. While calves are still lying up, their mothers are likely to be tied to a relatively restricted locality and spend a lot of their time with other females in the neighbourhood that are in the same condition. However, calves grow rapidly and within two or three months of birth are mobile and accompany their mothers within nursery herds, which reach their maximum numbers in December. The behaviour of animals within large groups is quite different from that of singletons or pairs. The latter are alert and easily frightened and will move away after a scare. Animals in nursery herds on the other hand, are more relaxed; they avoid close contact with other large herbivores and tend to make way for buffaloes, rhinoceroses and elephants, but they are relatively fearless, even of predators and I have



seen a female in a large nursery group make a very determined charge at a hyaena which was walking past. Prickett (personal communication) has seen one strike a giant hog that attempted to mob it. Herds numbering over 50 animals have been recorded in the Aberdares.

In the course of trapping bongo, Root (personal communication) observed a large herd remaining in the immediate vicinity while labourers constructed a temporary enclosure around a captured cow. In this case it is difficult to know whether the capture influenced the herd's behaviour or whether the site was a specially favoured refuge, or whether some other factor was at work. Under less extraordinary circumstances, both ecological and social influences can be seen to affect the pace of movement and the spacing of individual groups. For example the activity pattern of female herds is likely to be altered by the presence or absence of males, which in turn depends upon oestrus cycles. In May 1973, a period of minimal sexual activity and optimum feeding, an all-female group of 14 animals spent an entire night at the Yathabara salt-lick. Of course in larger groups individuals tend to take longer to satisfy their appetite for salt. Against this must be set the general condition of the vegetation and the female reproductive cycle. During lean seasons, feeding requirements force large groups to be continuously on the move. The nutritional needs of large animals dependent on high quality green stuff must largely determine the overall range, the pace of movement and the time the females can spend on activities other

Composition of bongo groups and their times of arrival at Yathabara glade. (Unsexed or untimed records and nights with visits by solitary animals or pairs only are not shown.) Oct.-Jan. 1975-1976. Note the close association of males with females: June-Aug. 1974-1976. Note the weak association between the sexes.



than feeding and ruminating, but it is clear that the degree of male interest in females also influences spacing. The timing and length of visits to the salt-lick in Yathabara glade reflect all these influences and they are seldom separable. Some animals simply appear to pass through ignoring the salt and are possibly on the track of other bongos that went by in previous hours or on a previous night. On nights when small groups of females visit in succession they are anything from half an hour to over six hours apart (mean three hours). This average spacing corresponds to that of groups of mixed sex recorded outside the peak mating periods. During mating peaks average spacing is reduced to less than two hours.

The influence of the principal mating period on social structure is best appreciated by comparing a chart of timed visits by groups of identifiable composition during October—January with comparable records for June—August when very few females are in oestrus (opposite).

Oestrous females are unlikely to play an active role in mating, indeed captive cows show signs of fearing the male and evade his approach. Xanten *et al.* (1973) have described captive males testing urine and playing the active role in courtship through persistent following and leaning against the cow. Captive males have been seen to make sucking movements towards the female's udder (Hillman, personal communication). This might help make her accept his approach. Outside the peak mating periods in April and November, the wider spacing of male and female groups could not only reflect less interest on the part of the males but also active evasion on the part of females and this in turn could influence activity cycles and the pace of movement.

Xanten *et al.* (1973) noted that both partners rubbed one another's sides with their heads after copulation, however the interest is not long sustained. Gestation is nine months (284 days). Growth is rapid and horns begin to show at three-and-a-half months, reaching about 13 cm by the age of seven-and-a-half months, when a captive male has been found to weigh 135 kg.

During the lying up period calves are vulnerable to pythons, (Verschuren, 1958a) leopards and hyaenas. Lions have been recorded killing bongo near the moorland zone of the Aberdares (Root, personal communication).

The principal predators of adults are humans, using snares or supported by dogs, spearing or shooting them when brought to bay. Prickett (1974) described them often taking to water, like a sitatunga, where they turn on their persecutors grunting and stamping.

The bongo has recently died out or is retreating in several of its few remaining refuges, notably Mt Elgon, South Kinangop and the Cherangani Hills (Price, 1969). This author pointed out that indentured labourers in the plantations and the sawmills and other new settlers relieve the boredom of weekends hunting with dogs and snares, techniques to which the bongo is particularly vulnerable (Ionides, 1948).

The bongo are also susceptible to disease, Simon (1962) wrote

"Bongo were thought to have been almost exterminated by rinderpest in the 1890s. This may explain the delay in the discovery of the East African bongo. If Wanderobo reports were true, the species may have suffered such heavy losses



from rinderpest that for a time bongo were exceptionally scarce . . . On the 12th of January 1913 a male bongo was killed in Kericho township, a few hundred yards from the boma. The natives did not have a name for it and stated that they had never seen another specimen, yet Kericho lies on the fringe of the Mau Forest Reserve which contains more bongo than any other part of East Africa."

It is interesting that the last known bongo on the Uganda side of Mt Elgon were killed in 1913—14. Large-scale and continuous hunting by Bagisu and Sebei hunters who live within easy reach of their haunts might have stopped this population of bongos from recovering from the rinderpest epidemic. Bongo populations reached a peak in Kenya during the 1920s and early 1930s and, according to Venn Fay were numerous as far south as Uplands and Matathia at this time. They are still abundant east of the Kinangop between Gatare and Fort Warwick.

At the present time human populations are dense near all the known bongo refuges and any relaxation or breakdown of the strict government protection they now enjoy would soon result in their extinction, for the animal is no longer protected by the taboos that may have helped its survival in the past. (The Azande, for instance, believed that eating the

meat of striped red animals caused leprosy.) Where conditions are undisturbed, they can become numerous and, in parts of the Aberdares, the Mau and Ivory Coast, are even a dominant member of the ecological community. They browse a large range of plants and thrive in captivity on hay, cattle cake and some green grazing and, once accustomed to confinement, they will breed in captivity.

Because the bongo is dependent upon a very unstable vegetation type, its long-term existence must be in doubt in those areas where woody growth is permitted to reach its climax. Conservation plans for the species should take account of its need for appropriate fodder and dense cover and it is important to gain some insight into the total range and spatial distribution of population units. Bongos could eventually be re-established in many parts of their former range, once their ecological role is fully understood and the habitat managed to their advantage.



Antelopes, Goats and Sheep

Antilopinae

Tribes

Neotragini

Cephalophini

Reduncini

Antilopini

Alcelaphini

Hippotragini

Caprini (and allies)

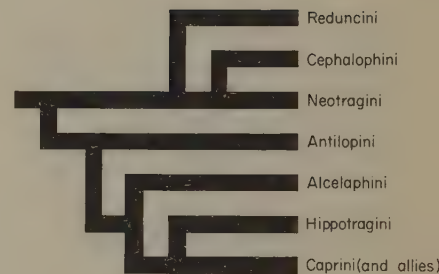
In this work I have gathered together an unusually large number of tribes under a single taxonomic umbrella. The Antilopinae in this expanded sense includes a more diversified grouping of antelopes than has been allowed by other taxonomists who have subdivided the group by all manner of permutations. Some of the reasons for reducing the bovids to two sub-families have been touched on (p. 9), but the substance of this arrangement will only appear in discussion of the constituent groups. This profile will concentrate on a single topic: the manner in which antilopine horns, their most obvious common characteristic, have been elaborated.

Several lines of evidence suggest that the antelopes traditionally classed as Neotragini represent contemporary survivors of a basal "eotragine" group (Piveteau, 1961), from which all the Antilopinae have evolved. For example, in most derivative lineages there is a marked tendency for the smaller forms to have more conservative traits (such as simple horns or less specialized morphology) than the larger ones. Efficient temperature regulation, which would seem to have been a significant innovation of the neotragine/eotragine basal group is found in all lineages and the Antilopinae embrace all arid-adapted bovids.

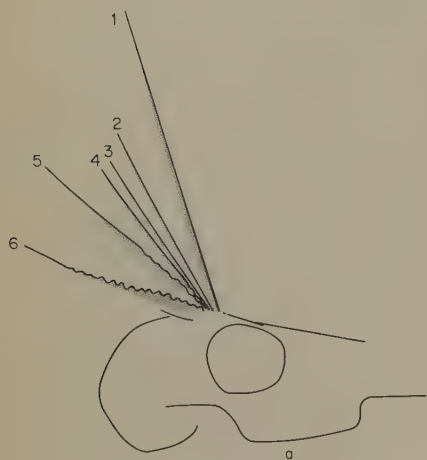
A high proportion of species have preorbital glands and there are in every lineage fossil forms with preorbital pits; evidence for the previous existence of such glands, even if they no longer exist in extant species.

But for a few specialized Neotragini, Cephalophini and Caprini, all members of this sub-family possess annulated horn surfaces and this characteristic has a functional link with elaboration of the primitive spiked horn. The group embraces all bovids with complex horn shape except for the smooth curled cones or keeled spirals of some Bovinae, shapes that have evolved according to quite different mechanisms.

In all bovid species ontogenetic horn growth begins with a smooth-surfaced straight spike but, of the African Antilopinae, it is only a few conservative neotragines and cephalophines that retain smooth, straight horns. If such daggers are at all long, their owners risk dislocation of their own necks with a deep stab into a struggling rival but the weapon can more easily be withdrawn if it is at a right-angle to the cranial surface. The longest



Relationships between Antilopinae as interpreted in this volume.



Evolution of the brow buffer illustrated by a gradient between upright, smooth stabbing horns and slanted corrugated horns in some neotragine antelopes. 1. *Pelea*; 2. *Raphicerus campestris*; 3. *Oreotragus*; 4. *Dorcotragus*; 5. *Ourebia*; 6. *Madoqua* and *Neotragus moschatus*.

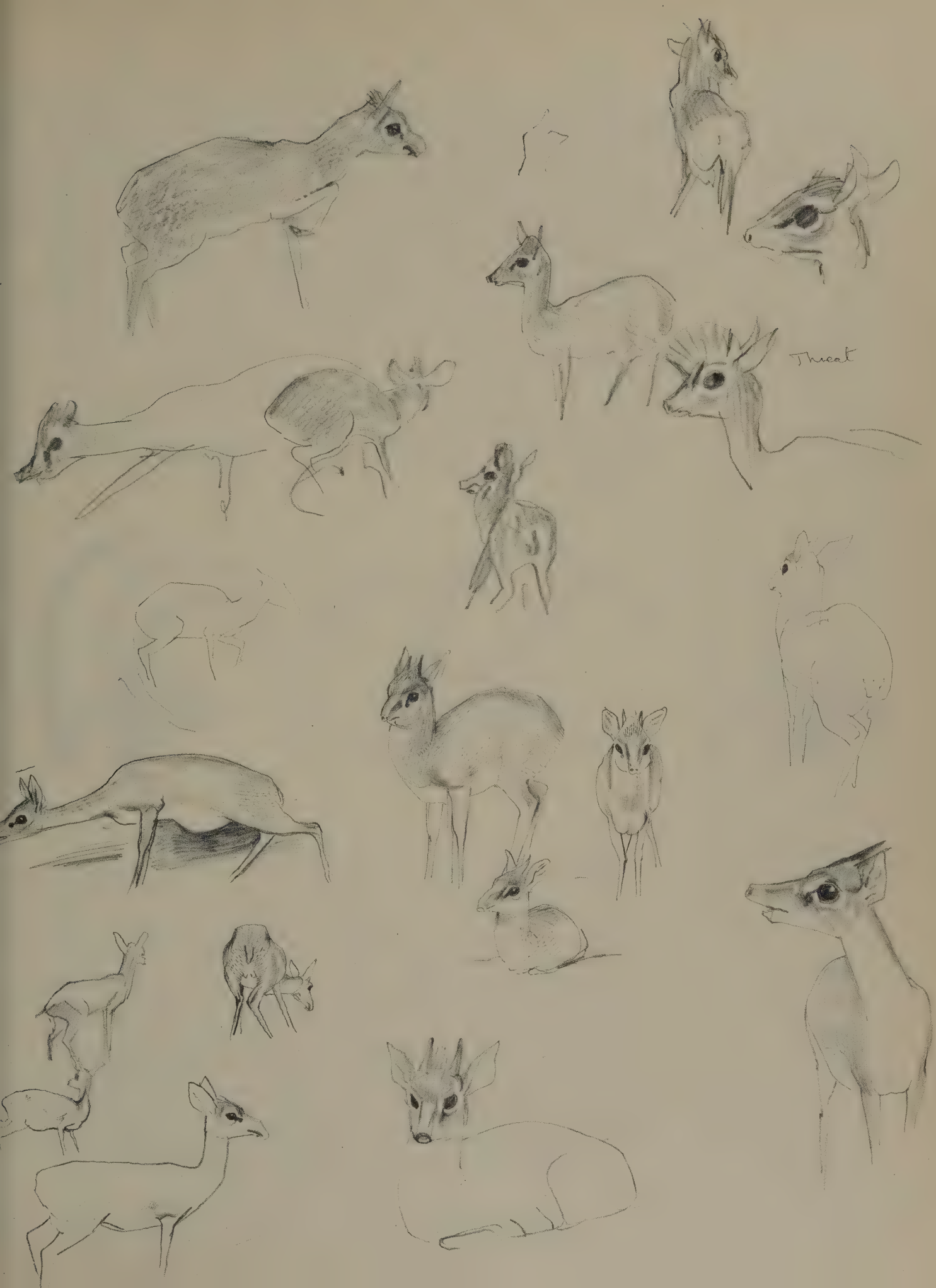
spike is possessed by male *Pelea capreolus*, (an aberrant species from the Cape, which is often included in the neotragine scrap basket). In this species allometric growth in the face (frontal, lachrymal and anterior maxilla) has elongated the face and so deflected the basi-cranial axis that the horns are exactly angled at 90° to the brain case. Territorial Cape rhebok have been reported to kill their rivals with unusual frequency during the rut, suggesting that intraspecific competition has found a rather wasteful and dangerous resolution (contributing perhaps to this species' relic status).

A comparison of the angle of neotragine horns in relation to face and braincase reveals a gradient with the longest smooth surfaced horns of *Pelea capreolus* being the most upright, whereas the more horns have developed annuli the sharper the backwards slope, thus diminishing the angle with the brain-case (see margin). The flattest horns are possessed by *Neotragus*.

A substantial difference in horn angle between *Neotragus moschatus* and *Pelea capreolus* is one of the morphological manifestations of different spacing systems. The latter live in large ranges on exposed pastures; being relatively large and lacking preorbital glands, they have limited means of marking territories with scent and are reported to be visually alert and vocal. In contrast male *Neotragus* scatter their small, visually obstructed home ranges with abundant tokens of their presence (primarily dung and scent from the pedal and preorbital glands). These olfactory deterrents tend to bias any confrontation with a rival in favour of the resident but the intimidatory effect of the males' glandular and excretory scents are backed up by horn threats which are part of boundary confrontation rituals. Ostentatious horning of branches or soil replaces a direct onslaught and these actions are closely associated with the ceremonial deposition of dung and preorbital scent. Since horning is also a spontaneous expression of male dominance and can take place at any time, conspicuously bruised vegetable fibres join glandular scent deposits as part of the multiplicity of landmarks in a territory. The activity incidentally helps to broadcast scent. Most species with annulated horns tend to grate or thrash their horns during dominance interactions and, at appropriate times, many appear to seek the rhythmic jolting of their head that results. However, these indirect or ritualized manifestations of horn threats are of low intensity. During a chase or fight, the rivals attempt to administer glancing blows to the body, and the corrugated surfaces and short low profile of the horns are evidently appropriate to this knuckle-duster function. Only at the highest intensities and in confined situations do *Neotragus* (and *Madoqua*) resort to stabbing with the horns.

There is a link here between horn shape and social organization. Scent-marked territories could only have arisen in small animals with relatively small areas to defend. Such systems are common to the Neotragini and Cephalophini, in both of which the functional importance of horns has been reduced. Virtually all duiker species have short stubby horns and they have retained primitive low-density territorial systems.

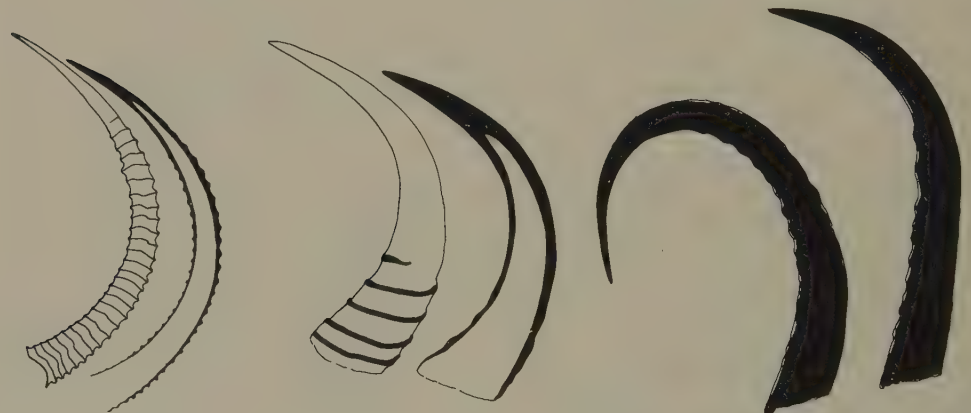
Switching from a stab to a glancing blow eventually proved to be a change of great significance in the evolution of Antilopinae, because scent-marking systems had to be partially or wholly abandoned as bigger animals enlarged their ranges in more open country. With the removal of olfactory prohibi-



tions such as those that help space duiker and suni populations, physical weapons once more came into prominence but it was primarily the corrugated shafts of the horns that were elaborated into sophisticated structures. Of course the spiked tip remained the ultimate weapon, but ritualized preliminaries to fighting or substitutes such as "cushion fighting", bush-thrashing and defaecation ceremonies probably first evolved in very primitive neotragines; retained or further elaborated in other Antilopinae they help to neutralize stabbing or restrict it to the occasional decisive fight.

Options for elaborating shape were severely limited at first—horn tips could remain straight, curl forward or backwards and these directions could combine with an outward flare or the shafts could remain close together. Shafts generally became thicker and in most lineages length tended to increase with size.

The later evolution of horns is described in some detail in the group profiles: splayed forward hooked horns in Reduncini (p. 321), simple staves or ramming curves in Hippotragini and Caprini (p. 540) and various combinations of ramming convex curves and catching concave hooks in Antilopini and Alcelaphini (p. 638).

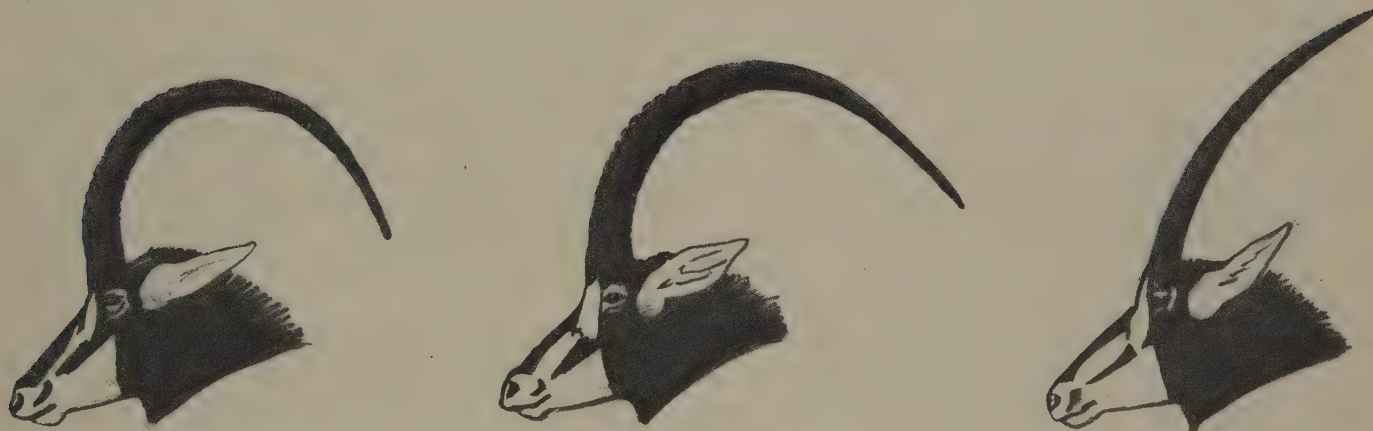


Growth arcs in sable and reed buck.
On right (in black) variation in curvature in horns of Bohor reed buck.

The astonishing variety of shapes found in modern Antilopinae started with simple distortions of a spiked bony horn core most likely in a diminutive territorial antelope. How could this have arisen? Within the living Neotragini horn corrugations are most pronounced in the secondarily dwarfed *Neotragus* and *Madoqua*, suggesting that annuli could have first appeared as an artefact of allometric growth (greater quantities of horn being packed on a diminished core). Whether this is their earliest origin or not, annuli represent rhythmically spaced and uneven deposition of keratin. It is the unevenness with which this material is laid down around the easily distorted horn core and the temporal rhythms of deposition that determine a horn's shape. Experiment may help to demonstrate the extent to which the traverse of a core is altered by unequal deposition rates in the sheath, but I suspect that it is only the more highly evolved species in which the core might be found to shape itself at all independently of the sheath.

Annuli provide a clear record of the pattern of the horns' emergence and indicate the relative rates of growth around the circumference of the horn. Longitudinal sections of horn allow this temporal pattern to be compared with the quantity of material that has been laid down. This technique demonstrates that a bend, such as the simple forward hook of a reedbuck horn, is the product of more material and a faster deposition rate at the back of the horn than the front. In the backward arch of a sable horn this pattern is simply reversed (see illustration). In both these species horn curvature varies individually and this appears to correspond with individual variation in the relative amounts of keratin laid down front and back.

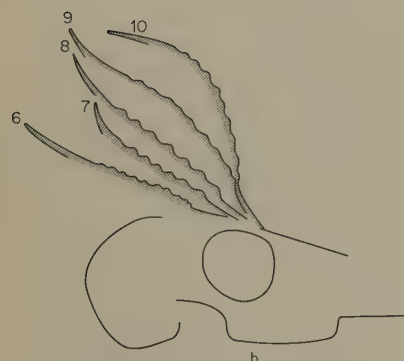
An upward curve to the horn tip in all species of Reduncini suggests that in any one lineage the earliest elaboration of the primitive spike and the associated fighting techniques (in this case stubby forward facing hooks used for grappling and head-wrestling) tend to condition all subsequent developments. I have already postulated that adaptation to a climatic and ecological gradient probably underlies the very early divergence of Reduncini from other Antilopinae. This divergence is also reflected in the basic structure of the horns.



The functional significance of splayed hooks is that contestants tend to come to grips without cushion fighting, horn grating or any other preliminaries. As Geist (1978) has remarked, horn wrestling and locking has arisen out of a defending animal's need to catching its opponent's weapons. This is consistent with the reduncines' long grass environment in that encounters may be sudden and vision obstructed. It is also consistent with the group's derivation from an ancestor in which the annulated stem was of less importance. In this connexion, an early suppression of land-marking with preorbital and other scents would have implied less significance for the ceremonial preliminaries that are so much a feature of male behaviour in other Antilopinae.

The caprine and hippotragine lineages probably derived from an early antilopine in which the principal common feature has been greater prominence for the corrugated shaft of the horn, produced by a combination of thickening, lengthening and upward arching.

Variation in curvature of horns in sable antelope.



Progressive elevation of the corrugated anterior surface in the horns of Antilopinae: 6. primitive condition, as in *Madoqua* and *Neotragus*; 7. Initial elevation primarily due to thickening of horn (tip upturns, as in some Reduncini); 8. elevation, lengthening and thickening of horn in primitive Antilopini, as in *Ammodorcas*; 9. elevation of longer, thicker horn with increased convex curvature, as in some *Gazella* spp. and *Litocranius*; 10. horn arched high above orbit as in some advanced Antilopini, Caprini and Hippotragini.

The primitive use of these arched, annulated shafts can be observed, even in large, advanced species as they attempt to bruise their opponent's body but, at an early stage of evolution, contestants fended off these attacks with their own horns and this ultimately led to direct clashing, which is such a typical feature of fighting most particularly in advanced caprines. At a very early stage in their emergence from a neotragine/eotragine stock, the Antilopini developed a type of horn that represented a structural advance on both the preceding types by combining closely parallel arches with hooked tips. This organization can still be seen in several gazelle species, with its most primitive characteristics often well displayed in the less elaborated horns of females.

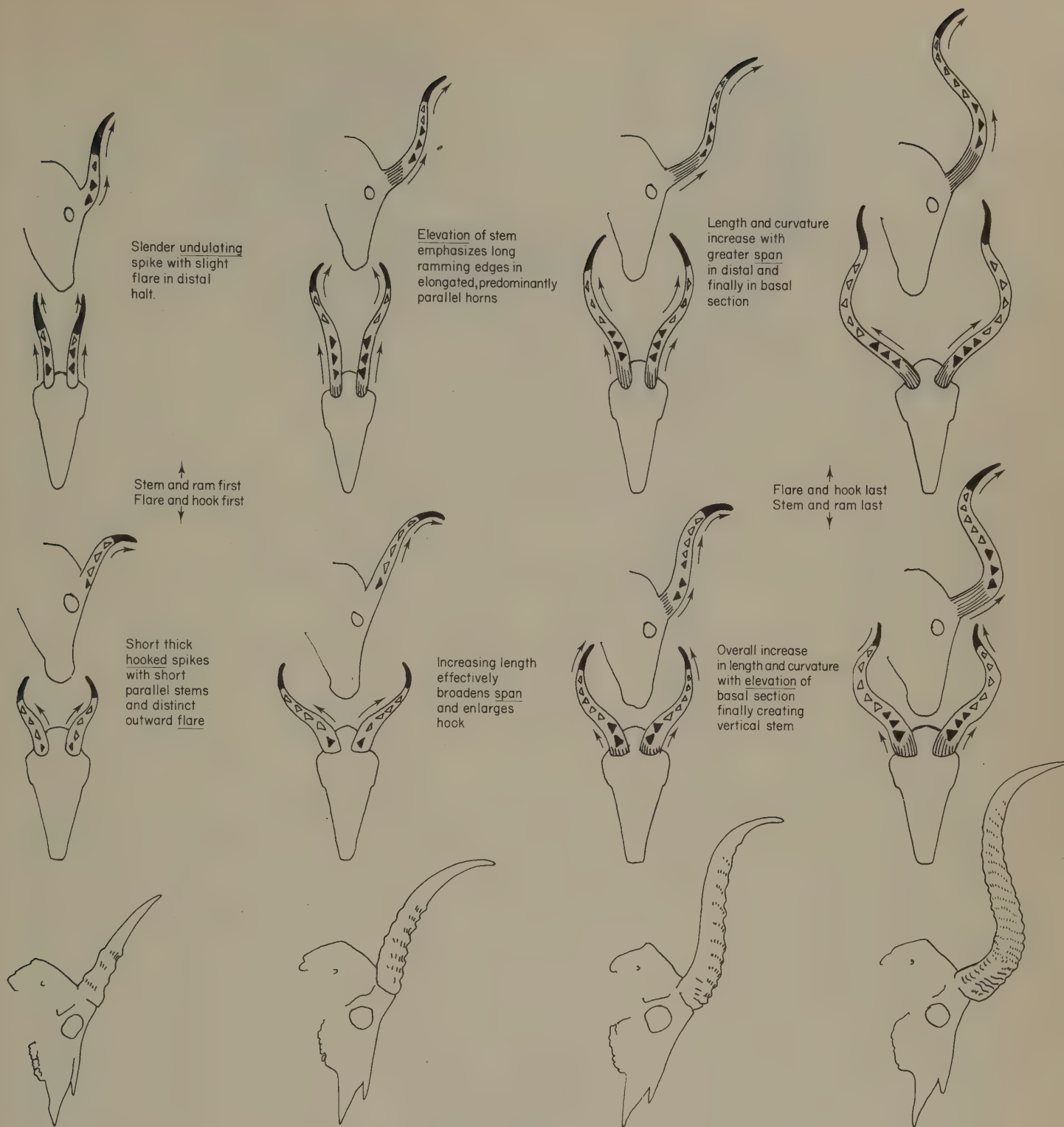
Whether the horns are used for offence or defence, the closer together the arches the more concentrated and accurate is the blow and the majority of caprine, hippotragine and antilopine species have progressively raised the horn arches up from the orbit.

The phylogenetic rising up of the horn arches over the orbit can be illustrated diagrammatically (margin), (there are also many specialized departures for this pattern, often involving horn bosses, cranial buffers or peculiarly hooked spirals, p. 438).

It has been suggested that the primary function of lumps, annuli and corrugations on antilopine horns is to provide a grip during fights (Walther, 1972a; Geist, 1966a). This is indeed their ultimate function during the ritualized fights of highly evolved Antilopinae, but the progression I have outlined suggests that this has been secondary to their original role as knuckle-dusters directed at bruising an opponent's body. Furthermore, the role of auto-stimulation during ritualized male-to-male encounters could have been significant in the evolution of corrugated horns and merits further investigation.

Functional analysis of the evolution of horn shape is complicated by convergence. For example, the hooked horns and large basi-occipital processes of *Ammodorcas* have led some students of the Bovidae to regard the dibitag as a highly specialized reduncine. A closer inspection of the horns in this species shows that they rise from the orbits for two or three centimetres before sweeping sharply back. Basal shafts are typical of the Antilopini, and that of *Ammodorcas* represents its minimal development whereas they were only developed in the reduncine kobs at a late stage of evolution.

The appearance of basal shafts or stems in the horns of *Kobus kob* can be correlated with increased frequency of fighting at higher population densities and the further ritualization that accompanies continuous male competition in very open, high-density situations. The shaft effectively adds another operational zone of buffer or battering ram to the horns and brings it up to the level of functional complexity that is found in Antilopini and Alcelaphini. The resemblance of the resultant lyre shape with that of the impala and some gazelles has been remarked on by many observers but a comparison of morphology in related species, extant and fossil, suggests that this remarkable similarity in shape came about through a progression of changes that had a difference sequence in each lineage. The sequence of changes is best suggested with a series of drawings (opposite). In the case



of the kob ontogenetic development of the horn recapitulates phylogeny so exactly that I have simply drawn an age-graded sequence of actual horns.

In the Antilopinae there would appear to be a relationship between population density and the size and complexity of horns which operates on very localized populations (p. 355) up to species level (p. 331). Selection for large complex horns would have been most intense in those populations

Convergent horn shapes in impala (top right) and kob (bottom right) with suggested sequence of functional stages in the evolution of horns. Functional zones as in diagram on p. 29. Actual ontogenetic development in kob horns shown in bottom row.





Impala *Aepyceros*.

that are likely to have maintained consistently high densities and where, regardless of the particular type of social structure, male competition is intense and direct.

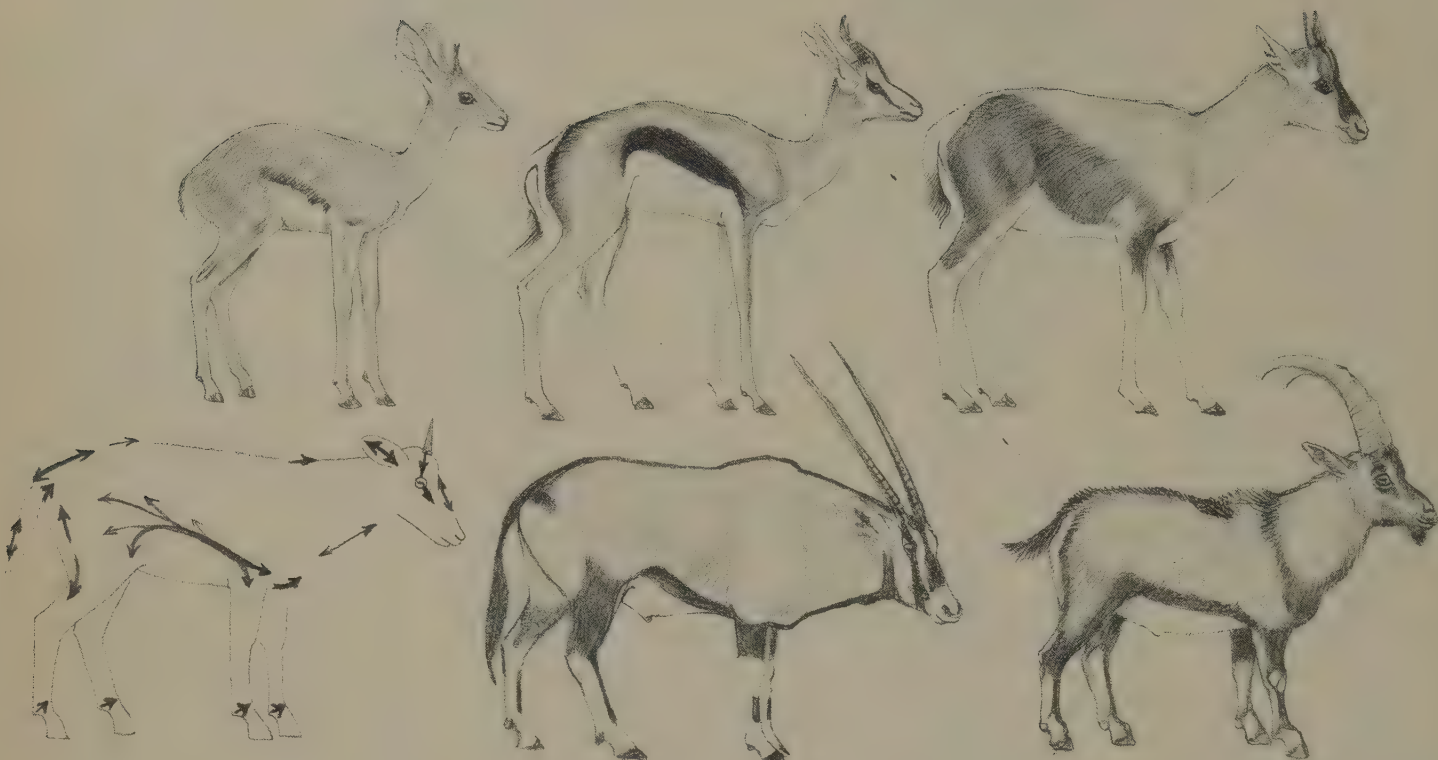
High density levels sustained over long periods are likely to intensify male competition and exert a great influence on the elaboration and enlargement of weapons.

Body size can influence horn shape in various ways. Animals that are relatively light, adept and agile, such as the kob and impala need well-differentiated functional zones on splayed horns that can readily catch and neutralize an opponent's onslaughts, as well as provide buffers, hooks and spikes for offence. Larger species, with greater momentum, need more heavily reinforced horns.

The nature of a horn's base on the orbit and the mode by which stress was transferred on to the skull were important considerations in the progressive enlargement of horns. Within the Antilopini there was a very early bifurcation between the gazelline antelopes that retained a solid connexion with the orbit and the antidorcine lineage which developed sinuses. The significance of this difference, which put an upper size limit on the horns of the former, is discussed in the alcelaphine profile.

A fundamental problem for many of the larger long-legged Antilopinae has been reconciliation of the instability that goes with long limbs with the need to maintain equilibrium during heavy-weight horn-bashing. The gerenuk has a unique and most ingenious head-nodding solution (p. 432), while all the larger Alcelaphini and Hippotragini have developed tripod fighting: dropping on to their knees but keeping the rear raised.

In seeking an explanation for such antelopes kneeling down to fight Maynard-Smith and Price (1973) invoked game-theory and made computer simulation analyses to suggest that "limited war" strategies benefited individuals in that retaliatory behaviour in their opponents decreased the fitness of aggressors. It is artificial to isolate the motor pattern in which horns are employed from the actual shape of the weapons because both are the product of closely correlated evolutionary changes.



In antelopes that are emancipated from camouflage increased contrast along the margins of countershading around genitals and along underside enhances conspicuousness. Horns, ears, face and hocks may also be elaborated.

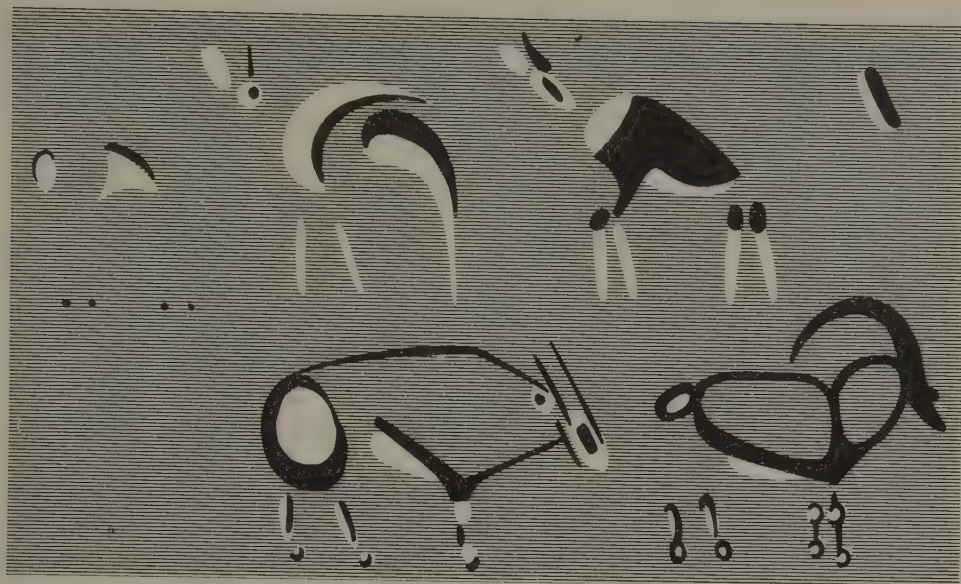
Above, this page: coat pattern in five tribes of Antilopinae. Top row: Neotragini (beira, *Dorcatragus*); Antilopini, (springbok, *Antidorcas*); Alcelaphini (bontebok, *Damaliscus*). Bottom row: diagram of pattern focii; Hippotragini (gemsbok, *Oryx*); Caprini (goat, *Capra*).

Opposite page: diagram of tonal contrasts in same species. Note increase in complexity of pattern from small, vulnerable and less social species to larger, safer and more social species.

Not all large antelopes have a limited theatre of war and the kneelers do not differ from other large herbivores in that behaviour and structures that were originally defensive in nature are capable of being changed and employed in peculiar forms of combat (see Vol. IIIB, pp. 4—72). Quite minor elements of behaviour and small structures can be transformed in this way and unique fighting styles and weapons will probably be best understood by reconstructing the evolutionary sequence of relatively small changes in morphology.

A kneeling position is primarily defensive in that the main advantage is stability in the recipient rather than the administrator of a blow, but the vulnerable instability of “standers” probably encouraged the ritualization of kneeling so that it became the normal position for both contestants in a fight. This change must have had considerable implications for fighting and horn shape. An extinct giant alcelaphine, *Megalotragus*, had an enormous span of horns which were probably used, like the water buffalo, to fence and push in a standing position. A wide span is unnecessary and awkward when the centre of gravity is lowered to a point nearer the ground and the field of conflict is cut down to the radius of head and neck.

In a kneeling position the apposition of horns can be very precise; the main force that can be exerted is a short but very powerful push which is generally followed or accompanied by an attempt to unbalance the opponent. The force of a push is transferred over a reinforced arch, stem or boss: throwing is achieved by some form of hook or arch. In *Hippotragus*



an arched hook combines both functions; the undulating horn of *Damaliscus* is only slightly more differentiated, whereas the horns of *Connochaetes* and *Alcelaphus* signify more complicated techniques of pushing, fencing and horn wrestling. Oryx instead minimize pushing and pack the full force of their powerful neck and shoulders behind stave-like blows from long straight horns. If these are not parried and strike home to the shoulder they jolt the recipient or even roll him over, in any case giving a painful measure of the rival's strength. Not surprisingly a plate-like shield has evolved through thickening and compacting of the neck and shoulder skin.

As with other bovids, elaborate dominance displays often seem to replace fighting or reduce its frequency, particularly in older, established males. Pattern and posture often play an important part in advertising dominance, and there is generally a good matching of rivals in antilopine fights, implying that the animals achieve a relatively accurate perception of size and strength before risking a fight.

Coat patterns are often very idiosyncratic and distinctive but the markings of some antilopine, alcelaphine, caprine and hippotragine species suggest either a common origin or at least a common mode of elaboration in their patterns. The rare neotragine *Dorcotragus* shows the rudiments of this pattern system (see above). In a more developed form it focuses attention on rump, flanks and head. At its most elaborate it tends to outline the neck or deepen the shoulder and polarize in highly specific markings on face and rump as in the oryx and agrimi goat. In the last two species "outlining"

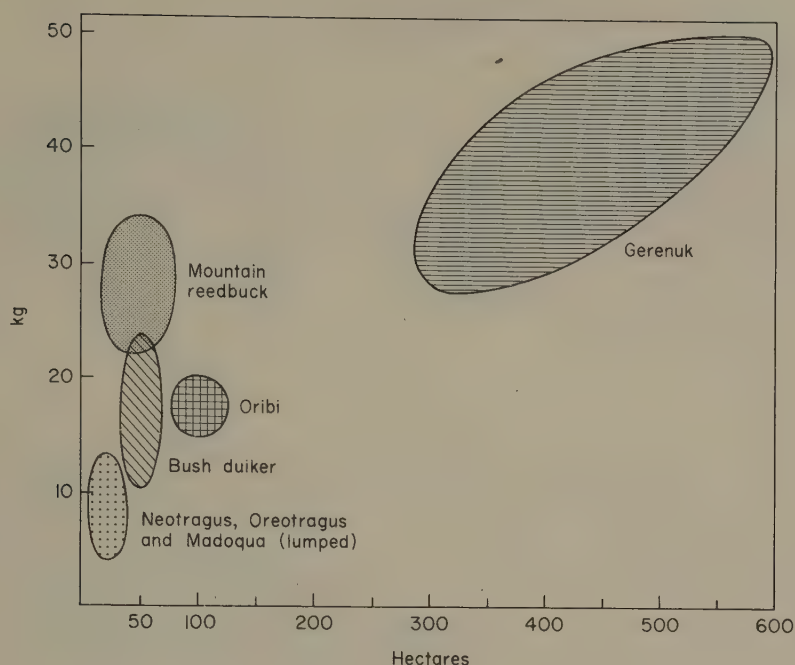
can be correlated with posturing in a lateral position during intra-specific displays (see Walther, 1974; Geist 1978). I have explored the process of elaboration and the function of distinctive patterns in greater detail for the primate genus *Cercopithecus* (Kingdon, 1980) and concluded that a need for optical clarity or coherence in signal transmission largely determines the way in which common genetic traits are elaborated into highly specific patterns. Similar considerations and modifications of the tints, length and orientation of hair tracts are likely to operate with the antelopes.

Detailed genetic and biochemical studies are beginning to contribute to our understanding of relationships within the Antilopinae and it is interesting that the primitive position suggested in this volume for *Raphicerus* and advanced status for the Cephalophini is supported by their chromosomes. Hard (1969) found a diploid number of 60 in the latter while *Raphicerus campestris* at 30 has the lowest diploid number recorded (Wallace, 1979).

The development of a relatively large brain in duikers is also evidence for a more advanced evolutionary status (Oboussier, 1979) but there is a special interest in the possibility that changes in brain size were initiated in phylogeny during a period of dwarfing. In other words, relatively large brains could have begun as a by-product of allometry. This possibility could have some relevance for human evolution in that a significant advance in relative brain size might have been associated with a period when some members of the hominid lineage (notably *Homo habilis*, or *H. afarensis*, from Afar) were particularly diminutive.

Body size has already been discussed in the profile of Bovidae and a link between small size and the possession of permanent territories was suggested. The difficulties faced by a large territorial species such as the mountain reedbuck during poor seasons (p. 346) suggests that outside exceptionally well-favoured habitats exclusive permanent territories begin to lose viability once the territory holder weighs over 20 kg and the area interest, therefore, in the gerenuk, which weighs between 30–50 kg and apparently succeeds in maintaining exclusive territories of between 300 and 600 ha in arid bushland (Leuthold, 1971a.).

The exceptionally efficient monitoring implied by a male's control of such large areas invites further study. The key to its ecological success seems to lie in scattered and minuscule portions of an unusually rich food source. Major sources of food for the gerenuk are species of *Acacia*, which tend to produce flushes in the dry season, particularly after isolated rain falls. *Acacia* species not only permit arid-land browsers to feed over most of the year but they also have exceptionally high productivity and nutritive value as well as tolerating heavy browsing. Pellew (personal communication) estimated that giraffes in Serengeti National Park may consume as much as 85% of the annual production of *Acacia xanthophloa* without critically damaging the trees. This species produces 5,000 kg dry weight per ha per annum (a production comparable with the best valley pastures). Young shoots of *A. senegal* have a crude protein content of 33.6% (Pellew personal communication). By comparison African grasses generally range



Range of individual territory sizes plotted against body mass in some antelopes with exclusive, permanent territories.

between 2% and 8% and protein values as high as 20% are exceptional in grass.

The significance of grass/concentrate diets in bovids was discussed earlier (p. 8) and it is interesting that as many as 60% of the Antilopinae species recorded from East Africa are concentrate feeders and only 35% are grazers.

Some contemporary survivors of the radiation of Antilopinae can conveniently represent older evolutionary grades and this should be borne in mind as we begin to recognize the deep evolutionary roots of plant-herbivore relationships. Pointing out that some plants, particularly grasses, have evolved adaptations that allow or encourage high levels of consumption, Owen (1980) has suggested that plants and the animals that feed on them are co-evolved and have developed mutualisms as intimate as that between a flower and a bee. This conception gains some credence from studies of grassland-herbivore dynamics on the Serengeti plains (McNaughton, 1979).

As the importance of plant-herbivore relationships gains recognition, Antilopinae, as the dominant large herbivore group in Africa, could prove an exceptionally rich field of study in the future.

In the profiles of tribes and species that follow there is much to suggest the common origins of all Antilopinae, but very detailed comparative studies of their palaeontology, anatomy, physiology and behaviour will be needed for an accurate definition of this very highly diversified group of antelopes.

Dwarf Antelopes

Neotragini

Genera

Neotragus

Raphicerus

Ourebia

Oreotragus

Madoqua

The living neotragine antelopes are an exceptionally fine example of an evolutionary radiation. All species are small and conservative but their morphological differences correlate well with a limited number of environmental and behavioural parameters.

These correlations have a broader significance because, as was pointed out in the bovid and antilopine profile, neotragines appear to be living survivors of a root stock out of which emerged a secondary radiation of advanced bovid tribes. In the initial divergence the most significant innovations made by this lineage were likely to have been more physiological than dietary in nature, and greater tolerance of heat and drought would seem to have been achieved by a small antelope with a conservative diet (mainly of leafy foliage) and a weight in the region of 10 kg.

Why should a small antelope have been the first to adapt to heat?

Wherever and whenever an early bovid was subjected to heat, selection for improved temperature regulation would have been strongest in the smaller animal because larger surface area relative to weight would lead to rapid overheating. Comparing body mass in a wide range of bovids it is striking that the weights of neotragine species are very tightly clustered and it would seem that retention of a body size close to that of the ancestral form has contributed significantly to an overall conservatism. The link between small size and the retention of a high nutrient diet and more primitive digestive system is due to the higher metabolic rate of a small mammal and the need to balance its greater energy losses.

The majority of living neotragine species live in habitats where their dietary needs can be met but where they risk exposure to heat stress. Cooling is achieved by a system of shallow nasal panting whereby venous blood is cooled by evaporation on the mucous membranes. The most extreme and best studied species is the dik-dik, *Madoqua* (see p. 249). Increased flexibility of the nose and reduction of the nasal bones are the most obvious signs of this mechanism and the reduction is greatest in the dik-dik. Species from cooler environments have their nasal passages more enclosed but sutures between the nasal and maxillary bones and the "waisted" shape of the nasals strongly suggest that there may have been secondary elongation from a more reduced condition (see overleaf). Such anatomical elaborations and secondary ecological adaptation are to be expected in survivors of a very ancient radiation, yet even within the 2—20 kg limits within which the neotragines



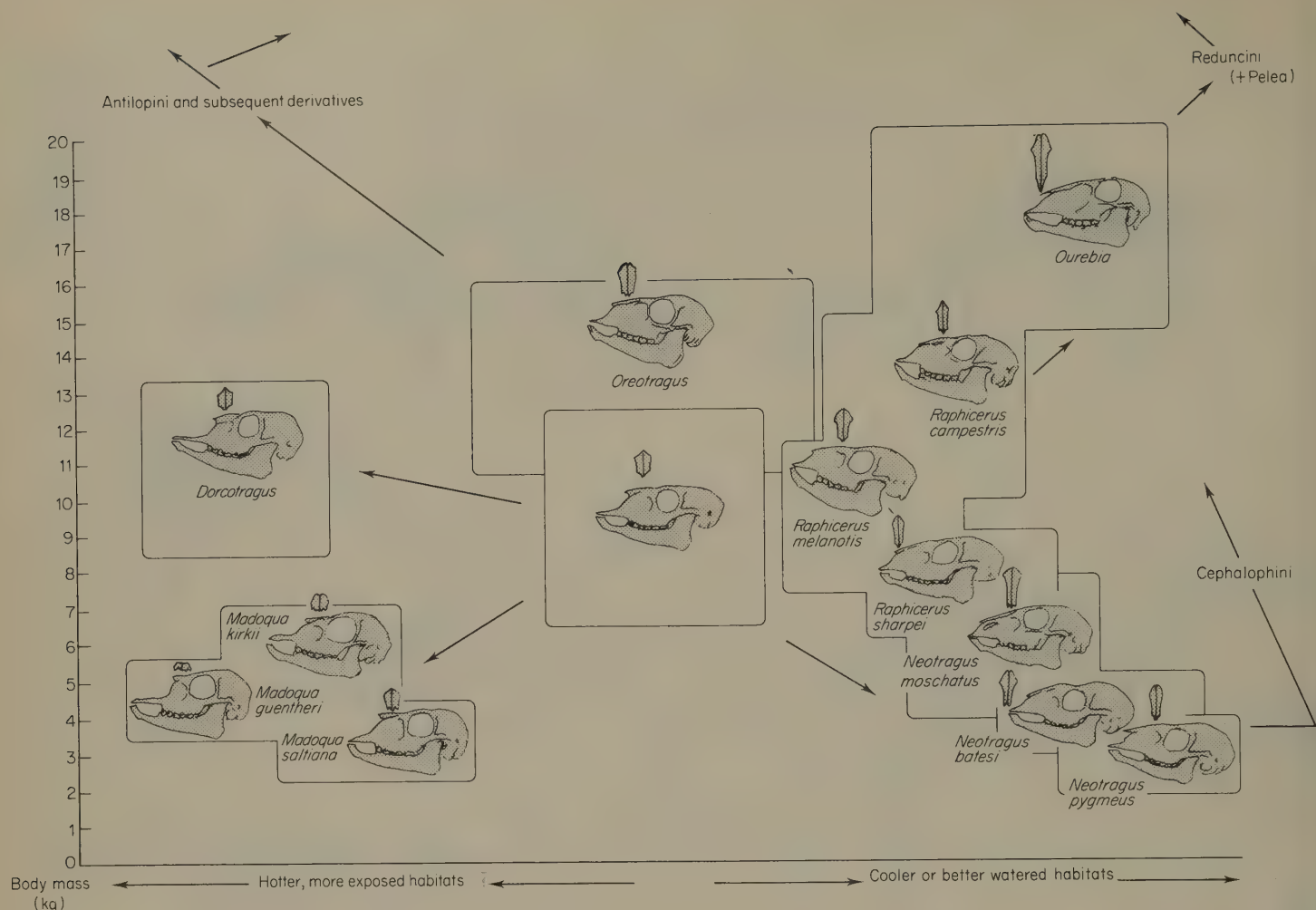
Beira, *Dorcotragus megalotis*.



are contained, small variations in dimension have combined with environmental differences to influence habits, nasal architecture, face and limb proportions and, to a lesser extent, the relative development of preorbital glands, orbits and auditory bullae.

For example, greater body size, poorer habitats or a combination of both can demand larger individual home ranges. This in turn can render the land-labelling function of facial glands redundant, as is the case for the beira, *Dorcotragus*, or, as in the oribi, *Ourebia*, subject them to still greater

Suni, *Neotragus moschatus*.



Body size and climate as major parameters in the neotragine radiation. Derivative lineages are indicated outside the 20 kg box.

demands (p. 217). In particularly difficult habitats such as the forest floor or in dry thicket there may be advantages for still further scaling-down and the minuscule portions and sparse distribution of low-level foliage help to explain secondary reduction in the size of pigmy antelopes, *Neotragus* spp., and dik-diks, *Madoqua* spp.

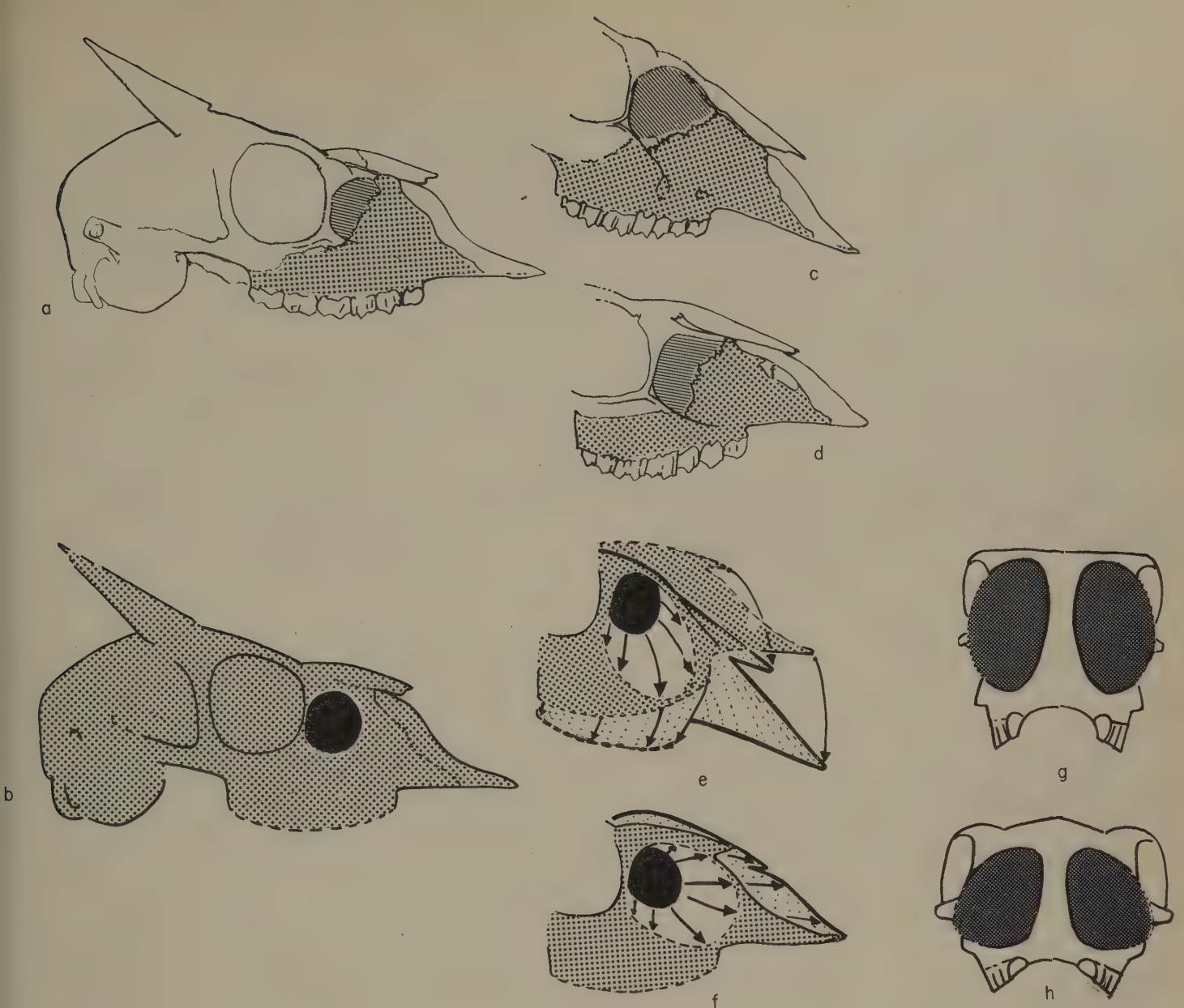
Other correlations between morphology, body size and climatic conditions are summarized in the schematic arrangement above, which uses the last two parameters as axes and lists basic attributes of the species. In the centre of this two-dimensional schema a point can be suggested which would have been occupied by a hypothetical neotragine/eotragine ancestor. Perhaps the closest of living species to this point are the Cape grysbok, *Raphicerus melanoitis*, and the Somali beira, *Dorcotragus megalotis* (both extra-limital to this study).

Morphological comparisons between the members of this array, particularly in respect of the skull, can be combined with study of *Eotragus* (see p. 12) to allow an extrapolation of the ancestor's skull to be made (using methods similar to those used in other volumes, i.e. Vol. II, p. 573; Vol. IIIB, pp. 15 and 122).

There is a general tendency to reduce nasals but the most extreme reduction occurs in the *Madoqua* lineage and *Dorcotragus*. The slender long-legged *Dorcotragus* and *Raphicerus campestris* have longish horns and more tapered



Reconstruction of ancestral neotragine.



muzzles but these traits are carried further in the oribi, where there has been a disproportionate phylogenetic increase in the length of the face and horns. In the oribi, expansion and deepening of the bony linings of the huge preorbital fossa has increased the distance between the upper margins of the maxilla and the orbits while the maxilla itself is also greatly elongated. The result is a very sharp downward deflection of the muzzle or bending of the basi-cranial axis.

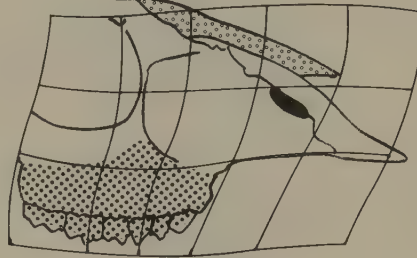
The situation can be compared with that of another large-glanded neotragine, the suni, *Neotragus moschatus*, where the glands' enlargement has not been accompanied by lengthening of the maxillary tube. A window or fontanella between the maxilla and premaxilla indicates that the latter bone has shifted back and arched up to meet the nasal. Where the two bones meet the nasals appear to have elongated from a shorter base. Enlargement of the preorbital gland may also have played a part in bulging the casing of the muzzle upwards, giving the suni its peculiar profile.

Influence of enlarging preorbital gland on skull shape in two neotragine species: a. lachrymal-maxillary junction; b. size and position of gland in an undifferentiated neotragine; c. lachrymal-maxillary junction in *Ourebia*, and d. in *Neotragus moschatus*; e. shows the outline of *Ourebia* muzzle superimposed on b. to show elongation, deepening and downward bend of the maxillary region (influenced by diet) and extension of gland; f. shows outline of *Neotragus moschatus* muzzle superimposed on b. In absence of maxillary elongation, the upper profile of the skull expands in correspondence with enlargement of gland. Cross-sections of glands in g. *Ourebia* and h. *Neotragus moschatus*.

Allometric growth in the muzzle of three *Neotragus* species a. *Neotragus moschatus*; b. *Neotragus batesi*; c. *Neotragus pygmaeus*.

The three species of the genus *Neotragus* demonstrate a simple allometric growth gradient that generates significant differences in skull form and explains why there has been distortion of the suni's premaxilla.

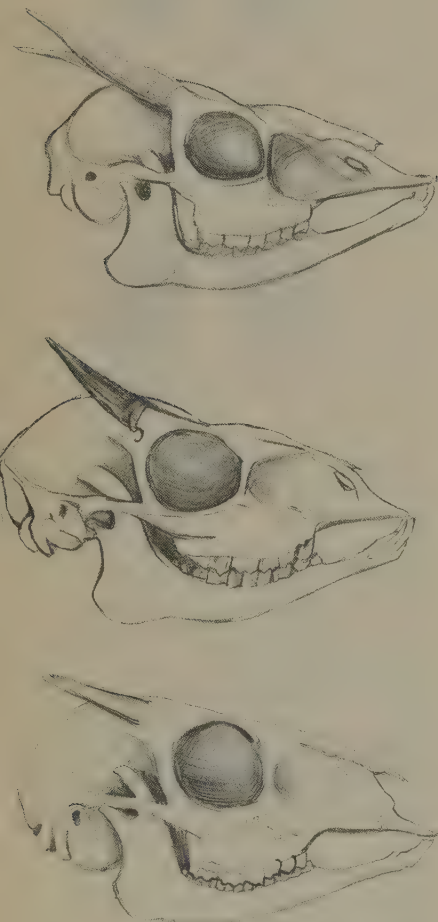
A progressive decline in size in this lineage has affected the nasals less than any other skull component, their absolute length remaining scarcely unchanged while the rest of the skull has shrunk around them.



Huxley (1932) distinguished positive from negative allometry in his discussion of the problems of relative growth. Subsequently Reeve and Huxley (1972) defined the latter with the term enantiometry. Although Huxley's study was mainly applied to ontogenetic growth, he followed D'Arcy Thompson (1917) in recognizing that the process was implicit in numberless phylogenies but there can be few lineages in which the phylogenetic effects of enantiometric growth are more clearly demonstrated than in the nasals of neotragine antelopes. The development might be correlated with the absence of heat-stress in forest, thus removing any selective pressure in favour of the nasal bellows mechanism.

Enantiometric growth might also explain the suni's relatively heavy battery of teeth. Feeding on tough foods, including roots, in the drier forests and thickets of eastern Africa, the suni's retention of robust teeth would have been selectively favoured. In moist forests further west such a disproportionately large tooth row is unnecessary and both *N. batesi* and *N. pygmaeus* have less robust teeth. It can be shown that contraction has been greatest at the front of the tooth-row and maxilla by imposing Cartesian co-ordinates on the skull profiles of the three species (see above). The co-ordinates also demonstrate that the premaxilla has suffered considerable distortion, bridging as it does, the interaction between static nasal tube and declining maxilla.

In the eastern African distribution of the suni and colonization of more homogeneous habitats by relatives that are further removed from the archtypal neotragine morphology, the *Neotragus* lineage typifies much broader trends in the radiation of neotragines and the larger radiation of cephalophines, antilopines, caprines and reduncines from this stock. A decisive factor in beginning these volumes and entitling this regional inventory an Atlas of Evolution was my realization of the significance of neotragines in bovid evolution and the key role of East Africa as an evolutionary theatre (see Preface of Vol. I and pp. 76—87). I have already pointed out that the majority of living neotragine species are distributed down the



Top: *Neotragus moschatus*; middle: *Neotragus batesi*; bottom: *Neotragus pygmaeus*.

eastern part of the continent with its dissected relief and exceptional range of habitats.

Preorbital glands are found in many bovid species and are not universally present in the neotragines, nonetheless they are more highly developed in oribi, suni and dik-dik than in any other antelope. Richter (1971a) has described them as being composed of two sets of cells. The black component of the secretion consists of lipoid droplets and melanin in the basal part of modified sebaceous glands. Coiled around these black cells are peripheral apocrine glands that secrete a transparent or slightly milky secretion and both gland segments reach the surface through the same two ducts. In addition to specific variation in size, the glands are much bigger in the males of *Neotragus moschatus*, *Ourebia* and *Madoqua* (corresponding to much more frequent use by the male).

In *Oreotragus* there is less sexual dimorphism in glands and both sexes exhibit frequent marking behaviour. (In this species females are sometimes horned, which also suggests a diminution in the strong differentiation in sexual roles which is general in neotragines.) Seasonal changes in size and activity of male glands has been observed which appear to correlate with sexual activity (Dunbar and Dunbar, 1974).

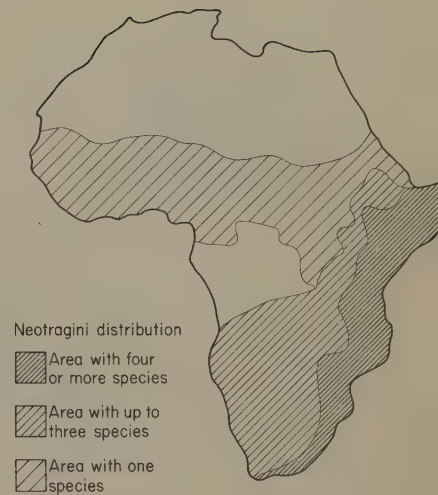
The preorbital glands are unlikely to have identical functions in all species and their detailed roles have been documented in only a few species.

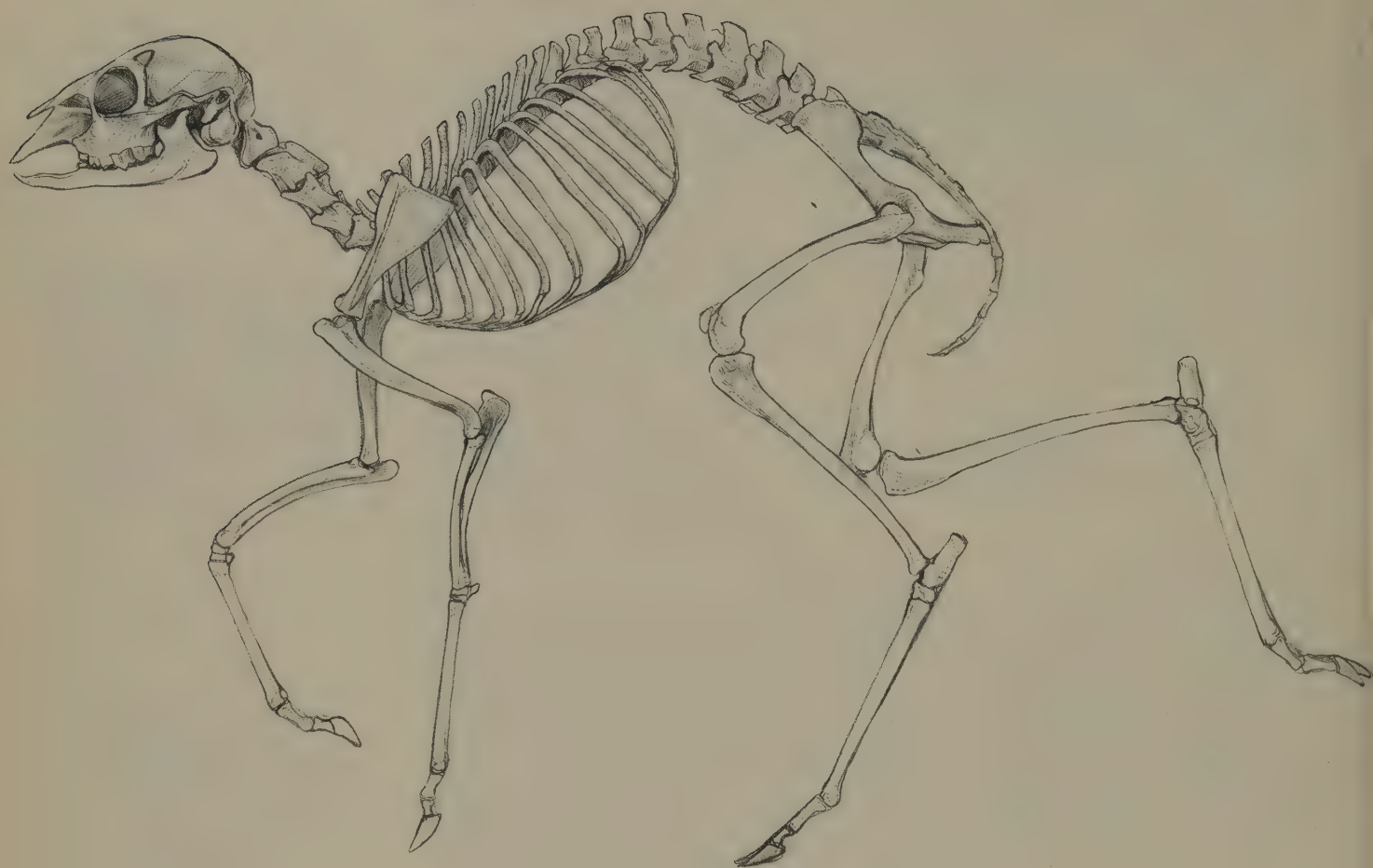
Noting a wide variety of scent-marking behaviours in mammals, Ralls (1971) related them all to intolerance and dominance. Whenever the glands are used to mark the environment this seems to hold true, but Simonetta (1966) described situations in which dik-dik that were known to be subordinate actually marked a dominant male with their preorbital glands. When female dik-dik mark other animals the message is more likely to be neutral and social. It is therefore probable that secretions are capable of providing several sets of information about an animal, its individual identity, its species, sex and age, its general and reproductive condition as well as some measure of its potential for aggression.

The effects of these signals on other individuals of the same species are likely to be strongly influenced by context, types of social situation, habitat and possibly by density.

The most universal situations in which a neotragine is stimulated to use its glands are the presence of another conspecific (particularly strangers) and any alien presence or unusual smell in its surroundings.

Preorbital signals are apparently capable of being perceived by taste as well as olfaction and in the klipspringer, dik-dik and suni I have seen pairs sniff one another's glands and sometimes lick them in what appears to be a check on identity. Such checks are frequent but the commonest form of olfactory checking is indirect, with an animal perambulating round his territory, here and there making a new deposit but mostly sniffing at the site of old deposits and renewing them. Thus in the territory of a dik-dik, suni, klipspringer or oribi there are scattered accumulations of these deposits which give abundant evidence of an animal's occupation. In the shared territory of a klipspringer pair both male and female mark their surroundings and in this way these strongly resident animals continually reinforce their familiarity with their environment and each other.





Above and opposite: skeleton and dissection of pigmy antelope, *Neotragus batesi*.

Preorbital marking is particularly common as a direct but ritualized response to the sight or scent of a neighbour when it is usually closely associated with an equally stereotyped dropping of dung (p. 223). In the dik-dik and probably in many other species this means that dung piles tend to accumulate and act as territorial boundary posts. Territorial male dik-diks also superimpose their dung on any strange smell in the territory after first sniffing and scraping vigorously. This includes the dung of familiar females, but since a male closely monitors the activities of the one or two females that live in his territory he is usually in attendance when they defaecate. In these circumstances he always scrapes and deposits on top of their dung in their presence and, once a female is well-established in a territory she will always visit one of the limited number of latrines and undergo the defaecation ritual. The inspection and defaecation ceremony is the major social interaction between sexes in the daily life of several neotragine species.



In the dik-dik, suni and oribi it is an opportunity for the females that live within a male's territory to have their familiarity with the male and his pheromones reinforced, and this is of critical importance because it is his marking activity that very largely defines the limits of their own existence.

In the dik-dik a territorial male is not only intolerant of other males but he will chase off strange females as well so that the females' existence is even more tightly controlled by the dangerous, sharply horned male.



Suni, *Neotragus moschatus*.

In the oribi the use of scent reaches its apogee. This species has a larger battery of glands and scents than any other antelope. An over-simple explanation is that if the larger territory of a larger animal must be scent-marked the demands upon the animal's anatomy and physiology must be increased proportionately. However the implications of this elaboration are more complex than that.



Oribi, *Ourebia*.

The oribi retains many features of a small neotragine, yet it has moved out into habitats where tallness and fleetness are imperative and they are taller, heavier, faster, larger-horned and more wide-ranging than any other neotragine. Increasing body size and proportional lengthening of the horn has made a dangerous neotragine male more dangerous (particularly to other males). If the males attempted to control directly the movements of females within their relatively large territories this would be both physically perilous for the females and generally wasteful of energy.

How then do oribi males compete for reproductive opportunities? The answer has been to intensify and ritualize still further some of the typical neotragine scent-marking behaviour. The occupants of a territory are even more persistently exposed to a particular male's scent. Within a territory the residents are continuously bombarded with familiar olfactory signals and both sexes avoid trespass very largely because they would be stepping outside this scented kingdom. Other neotragines tend their olfactory fences and avoid fighting outside them, but oribi have replaced direct attacks with ostentatious pre-orbital marking more completely than any other species. Suni have also transformed direct fighting into ritualized scent-marking but are more prone to horn surrogate rivals in the form of branches and bushes, meanwhile vigorously licking their own facial glands. Dik-dik also

show ritualized horning but preorbital marking is less consistently reciprocal and can lead to threats with raised crests, "cushion-fighting" or an actual attack.

Wherever a female's home range has been demarcated by the activity of a male she is more likely to be mated by that male but the oribi is perhaps the most extreme of neotragines in that he so saturates the environment of one or more females that they cokabit voluntarily, thus ensuring reproduction and avoiding direct competition among males for oestrous females. The latter are therefore not subject to stress or coercion (p. 225).

Although many species use neutral feeding and refuge areas outside their territories (and may be forced to desert the latter periodically), there are many advantages for all the residents in an established territory, particularly in relation to reliable sources of food and escape from predators.

The familiarity that is given to a territory by the male's olfactory marking exerts its stay-at-home effect on the juveniles growing up there and the tendency for the males of most species to be accompanied by more than one female is generally due to female offspring staying on.

In all species the first sign of horns in a young male elicits persecution from the territory holder and an increase in the frequency of marking. Elaborate appeasements by the adolescent may delay the expulsion but the youngster is normally driven off when between six and nine months of age. At about this age an animal is sexually viable but readiness to enter the lists for a territory is signified, at a year to a year-and-a-half, by mature weight, by the horns reaching functional length and breadth, by a moult into adult pelage and by filling-out of the preorbital glands.



Suni, *Neotragus moschatus*.



Dik-dik, *Madoqua kirkii*.

The fortunes of a male from the time of his expulsion to the time he establishes his own territory have not been studied in the wild but it must be a critical period and one in which species may differ in timing and in resulting sex ratios. For example, there is some indication that older oribi may be at an advantage over younger ones in some habitats. If captive studies are any indication, year-old dik-dik and suni are instead very effective candidates for territory.

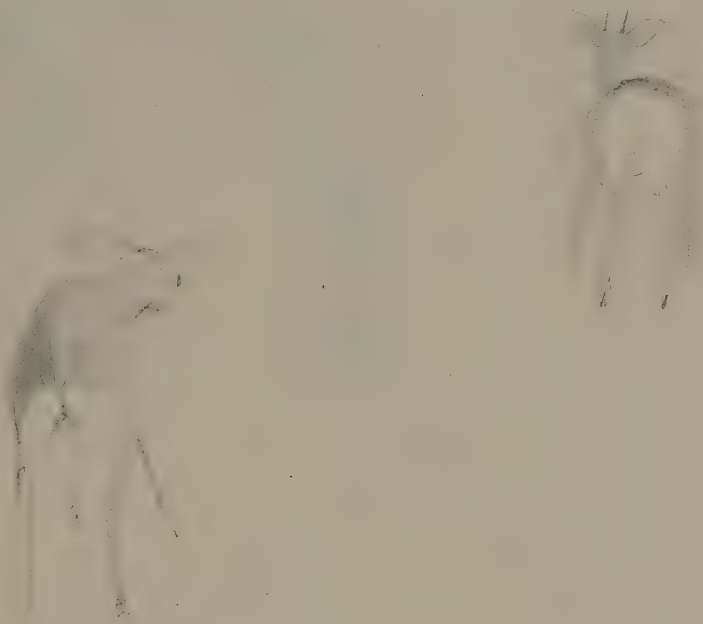
In addition to olfactory communication, neotragine antelopes employ vocal and visual modes. They make a variety of squeaks, screeches, snorts and barks and the infants of some species may use ultrasound. In the course of dissecting out a dik-dik's nose to investigate its thermo-regulatory function I found turbinals which seem to have been modified to act as whistles (figured on p. 250). This species in common with oribi and klipspringer makes a shrill whistle, almost certainly through the nose. The special interest of this is that the primary adaptation of heat regulation involves control of air in the nasal area. The elaboration of turbinals to produce sound by the same basic mechanism may have been a useful by-product of what was primarily a physiological development.



Signal patterns for visual communication are better developed in populations that are less subject to predation. The brightest colours and contrasts are found in some localized races of *Madoqua saltiana*. The dik-dik's crest, which occurs in both sexes and which hides the horns of the male when fluffed out, may serve as an early warning threat signal. Usually fanned by dominant individuals at the beginning of an aggressive encounter, the crest may serve to avoid potentially dangerous confrontations or channel them into ritualized display. Since territorial dik-dik are intolerant of both sexes, most adolescent animals are likely to experience the association between horn strikes and a fanned crest. Subsequently the fanning may serve female rivalries as well as male and I have seen penned females successfully drive off rivals for food by advancing with raised crest.

Flaring of fur in the anal area instead appears to signal appeasement and conspicuous circular patches appear on the rump of *Madoqua* and, in a less obvious way, of *Raphicerus* and *Neotragus*. *Oreotragus* instead has no rear-view signal at all.

Most neotragine species are locally abundant in favourable localities but, because all are territorial, they are particularly vulnerable to snaring and hunting with dogs. The long-term conservation of local populations, particularly of the oribi, may need regular reappraisal. The special phylogenetic interest of two relic species not found in East Africa should be mentioned and efforts should be intensified to ensure that both *Dorcotragus megalotis* in Somalia and *Raphicerus melanotis* in the Cape are given adequate protection. Perhaps breeding colonies of these species could be established and both deserve intensive study as species close to the centre of the neotragine and antilopine radiations.



Above, steinbuck, *Raphicerus campestris*.

Opposite: klipspringer, *Oreotragus*.



**Pigmy
Antelope
(*Neotragus
batesi*)**

**Family
Order**

Bovidae
Artiodactyla

**Measurements
head and body**

50—57.5 cm

54.7 cm *N. b. batesi* female average

51.2 cm *N. b. batesi* male average

height

24—33 cm

31 cm *N. b. batesi* average

tail

4.5—5 cm

weight

2—3 kg

2.8 kg *N. b. batesi* female average

2.2 kg *N. b. batesi* male average

horns

2.2—3.8 cm

Note: The eastern race, *N. b. harrisoni*, is somewhat larger than *N. b. batesi* but average measures are not available.

Pigmy Antelope (*Neotragus batesi*)

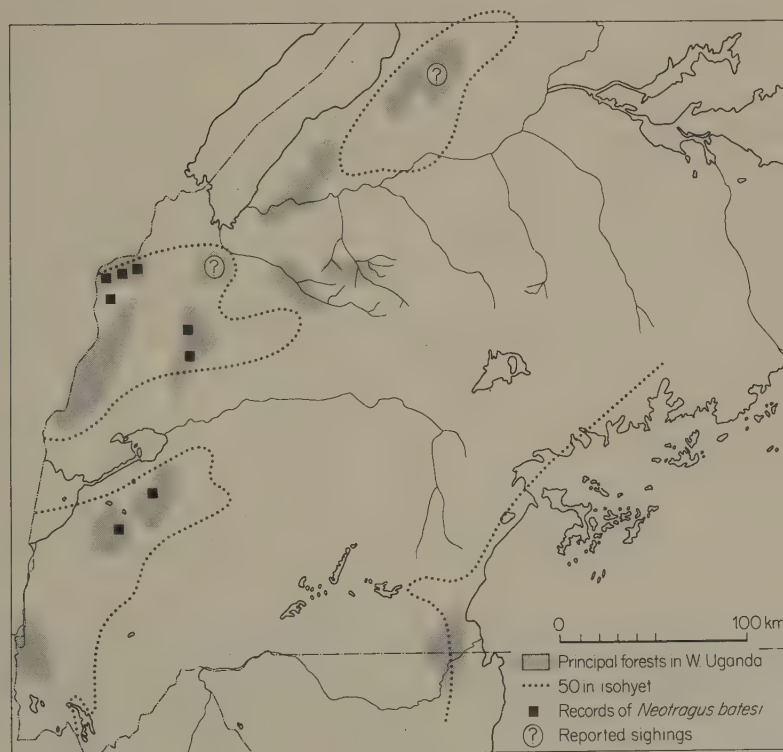
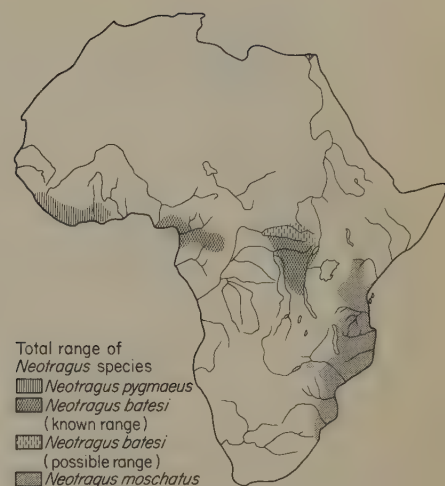
Race

Neotragus batesi harrisoni (synonym: *Hylarnus harrisoni*).

This diminutive animal is the smallest ungulate found in East Africa. A rich mahogany-brown with a shiny gloss to the fur, it is inconspicuous but nonetheless the black and white markings of the ears are quite precise and geometric as are the white chevrons on the throat.

The distribution of this species is restricted to the Central and Cameroon-Gaboon Refuges and it is one of the indicator species for these refuges, which were discussed earlier (Vol. I, pp. 65—68).

This little forest dweller is subject to severe ecological restrictions. It is certainly scarce in those Uganda forests in which it occurs, particularly when compared with the blue duiker. I have only encountered it six times, and on every occasion the animals were seen in areas of dense, low undergrowth near water courses, roads or in areas regenerating after logging. The female figured opposite was collected at 10 p.m. on the edge of the forest. Cultivators in the vicinity were familiar with nocturnal visits from these antelopes and showed me the nibbled leaves of their beans, sweet potatoes and groundnuts. In the Bwamba forest they occur along forest edges and under low canopy *Cynometra* (see Vol. I, pp. 45—50), and Boulière and Verschuren (1960) described them from swamp forest, *forêt sèche*, and





} Margins of secondary forest

Area of home range in secondary forest

Area of home range in unweeded cocoa gardens (Vegetation more than 30 cm high.)

Area of home range in weeded cocoa gardens. (Vegetation less than 30 cm high.)

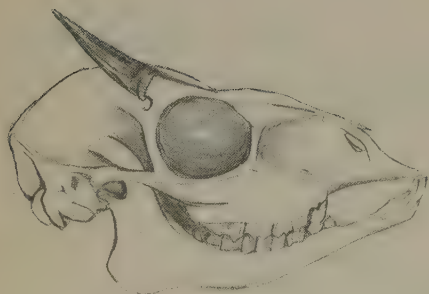
• Diurnal activity records

○ Day resting spots

■ Nocturnal activity records

□ Night resting spots

Home range of a female *Neotragus batesi* in North-east Gabon (from Feer, 1979).



rain forest. Rahm (1966) described them from low and medium altitude forests in eastern Zaire. Therefore, so far as the habitat of *N. b. harrisoni* is concerned, this race is not without some adaptability.

The question of the species' limited distribution within forests that show no very visible differences has been considered by Feer (1979) who concluded that rain during the dry season might be a major limiting factor. Low-level herbaceous vegetation is probably affected very quickly by local seasonal patterns which do not show up in gross rainfall figures, thus a prolonged dry season following the short rains may be more deleterious than a shorter one following the main rainy season. Thus *Neotragus* occurs near Yaounde, Cameroon, with the second pattern, but is absent from Makokou and other Gabon localities with the first pattern. Feer correlated the distribution of *Neotragus batesi* in northern Gabon with the 25 mm monthly rainfall isohyet at the height of the dry season, in July.

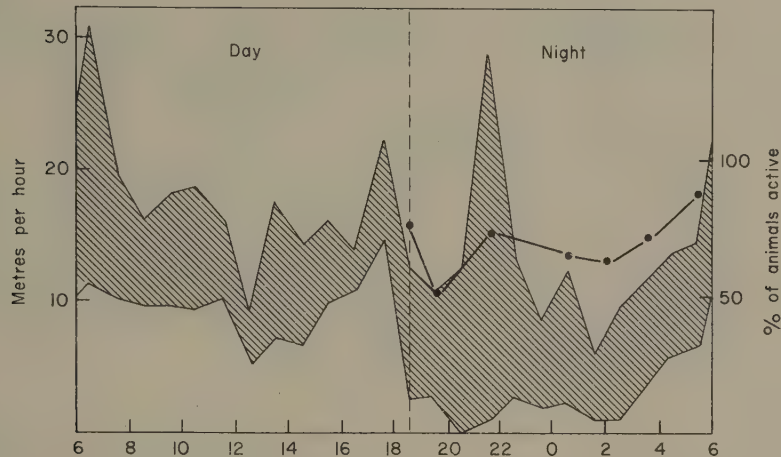
In the Mekambo area of north-eastern Gabon subsistence agriculture and plantations of cocoa and coffee encourage a year-long abundance of weeds and the existence of a local taboo on the hunting of pigmy antelopes allowed Feer to study this species in a peculiarly undisturbed situation. Without the agency of man or elephants it is difficult to find restricted areas of forest in which palatable plants will produce fresh growth throughout the year and at levels accessible to a pigmy antelope. Even in the ideal conditions at Mekambo Feer found that an animal rotated its pastures, spending one or two months in one part of its 2–4 ha range before moving to another area (see margin).

The need to find adequate quantities of nutritive and digestible foliage influences not only longer-term range patterns of the pigmy antelope but also its daily activity cycle. Of the 31 species of dominant plants which produce foliage at ground level, Feer found only 29% were heavily browsed by pigmy antelope and animals were probably feeding on and off throughout the 24 hours, as they were almost continuously active. In Uganda, I too found the species active day and night. Nocturnal invasion of plantations and gardens is as marked in Gabon as in Bwamba and Feer (1979) was able to radio-track a number of individuals and not only demonstrate that the animals were active throughout the day, in spite of being hidden in dense cover, but also he was able to show that their daytime refugia (59% of their total home range) corresponded with denser vegetation with a mean height of 124 cm. By contrast, their less dense nocturnal pastures amounted to 28% of their range and the vegetation had a mean height of 26 cm. Only 13% of their range tended to be used regardless of day or night.

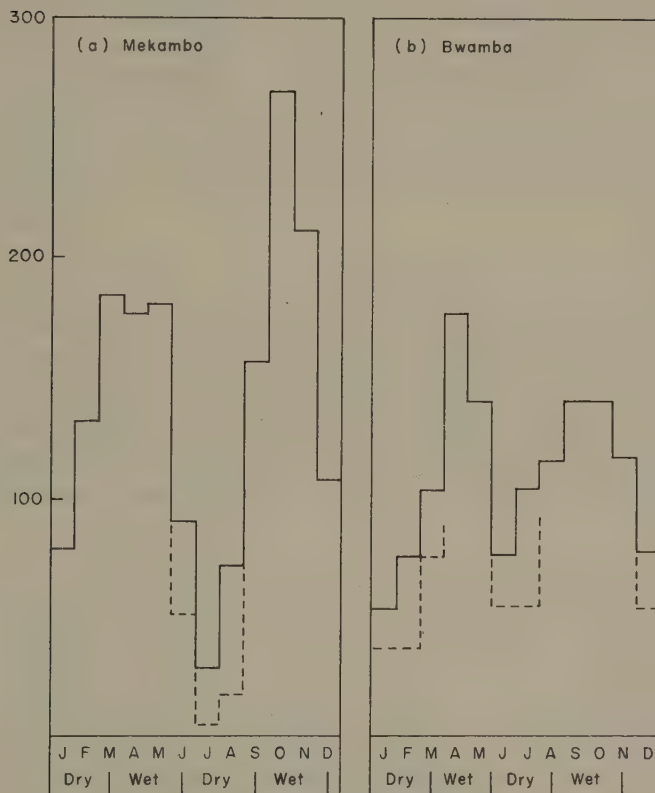
The tendency to feed in recently cleared gardens, more open plantations and road verges during the night is probably due to greater security and to reduced disturbance.

Of cultivated crops more favoured in Gabon the foliage of sweet potatoes, *Ipomoea batatas*, yam, *Diocorea*, old cocoyam, *Colocasia*, and various peppers, *Capsicum* spp. are listed by Feer. Of dominant or abundant species of the forest, the acanthus, *Brillantaisia vogeliana*, and the cucurbit, *Momordica cissoides*, are heavily browsed by pigmy antelope and Feer also recorded a preference for *Phaulopsis micrantha*, *Cyathula prostrata* and various fern species; 55% of the plant species available were not eaten at all.

Feer recorded pigmy antelopes moving an average of 500 m in 24 hours; his radio records of small scale movements were the principal indication of an activity pattern which showed three peaks, one at dawn, one at dusk and one about three hours after dark (see below).



Activity of *Neotragus batesi* in North-east Gabon as suggested by the maximum-minimum movements (in metres per hour) of five individuals (hatched area) compared with a histogram of their nocturnal activity represented as the percentage of animals active (from Feer, 1979).



Annual rainfall pattern in two areas inhabited by *N. batesi* a. Mekambo (Gabon) and b. Bwamba (Uganda). Rainfall minima in two neighbouring localities are indicated (dotted lines). Longer more intense dry seasons and their effect on low level herbage are thought to be the main factor excluding *Neotragus batesi* from Makokou in Gabon and Mubende in Uganda. (In part after Feer, 1979.)

The animals are predominantly solitary and in the Mekambo area, where densities are likely to be maximal, Feer reckoned neighbouring females were on average 150 to 190 m apart, which represented the distance between their core areas. Of the twelve females in his study area eight shared an



area with one or two other females and where there was a shared, or partially shared range (which might denote a blood relationship), animals were 55 to 100 m apart. Calculations based on home range areas gave an average density of three animals for four hectares or 75 per sq. km, but other estimates for the population gave 35 animals per sq. km, however, such densities could only be attained in exceptionally favourable parts of the habitat.

Females amounted to 60% of the Mekambo population and males probably overlapped at least two female ranges each, as they covered a larger area and no overlaps in the ranges of adult males were recorded. There was no evidence for male to male relationships. Only males mark their home ranges with secretion from their highly developed pre-orbital glands and they are almost certainly territorial. Two adult males have been seen some 50 m apart and torn ears suggest fighting is not uncommon.

Males carefully smell or lick twig ends before inserting them into a pre-orbital gland and all suitable twigs along their way tend to be marked with gobs of secretion. Feer did not observe any ritualized behaviour associated with defaecation or urination and he concluded that there was no obvious marking role for faeces or urine. This is in marked contrast with the suni and dik-dik.

A short series of panting, raucous barks is sometimes made when fleeing and, as in other bovids with spaced-out territories, the cries may alert neighbours to the author's position as well as alerting them to a disturbance or danger. Flights are of short distance and duration, followed by freezing and then a slow high-stepping progress through the undergrowth. Difficult obstacles can be cleared by a leap.

Captive youngsters make a repeated nasal moan and this is the normal communication between a mother and her young, the adult's voice being lower in tone. Males seeking a female make a similar but more nasal call, but cease once they are in contact; the female does not reply to the male's call.

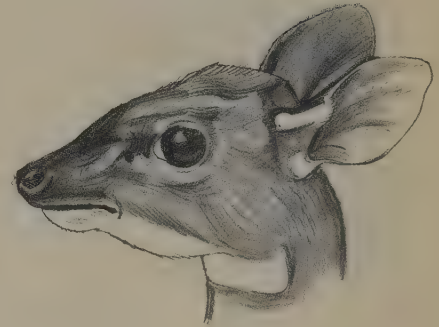
Contacts between the sexes have not been observed in the wild, but mating is apparently sustained throughout the year with two peaks straddling the latest dry and early wet seasons. Gestation is thought to be in the region of six months and the two birth peaks appear to occur in Gabon at the end of one rainy season or the beginning of a dry one. Feer considered that the benefit of the young being weaned at the beginning of the following long rains, when food is most abundant, might be a major determinant for this breeding pattern.

A lactating female and juvenile of the eastern race, *N. b. harrisoni*, have been collected (separately) in the Bwamba forest in June. Bourlière and Verschuren (1960) recorded a full-term foetus in early April and Rahm (1966) recorded a young one in March for eastern Zaire.

Owen's account (1973) of the rearing of a female *N. pygmaeus* pictures an animal with many resemblances with this species and the suni but she found that growth was abnormally slow, as the animal took more than a year to attain full size.

The major predator is likely to be the crowned hawk eagle, *Stephanoaetus coronatus*, but golden cat, *Felis aurata*, leopards and pythons might take them on occasion.

Although it is occasionally captured in snares and nets, *N. batesi* is sufficiently rare in Uganda for it to be virtually unknown by anyone but the more experienced forest hunters in the Kalinzu and Bwamba forests. Like the other forest rarities this species is threatened by habitat destruction and changes in forest management. (See Appendix and insert Vol. I, p. 46).





Suni
(Neotragus
moschatus)

Family
Order

Bovidae
Artiodactyla

Local names

Suni (Kiswahili and Kichagga), Kasuni
(Kikuyu and Masai).

Measurements
head and body

58—62 cm

height

30—41 cm

tail

11—13 cm

weight

4—9 kg

horns

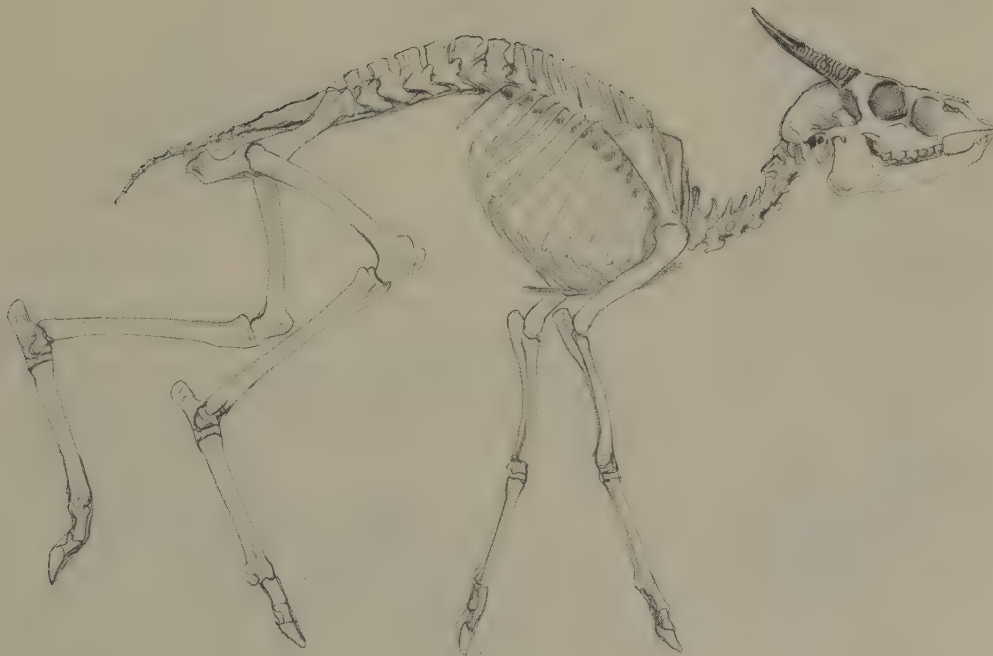
5—13 cm

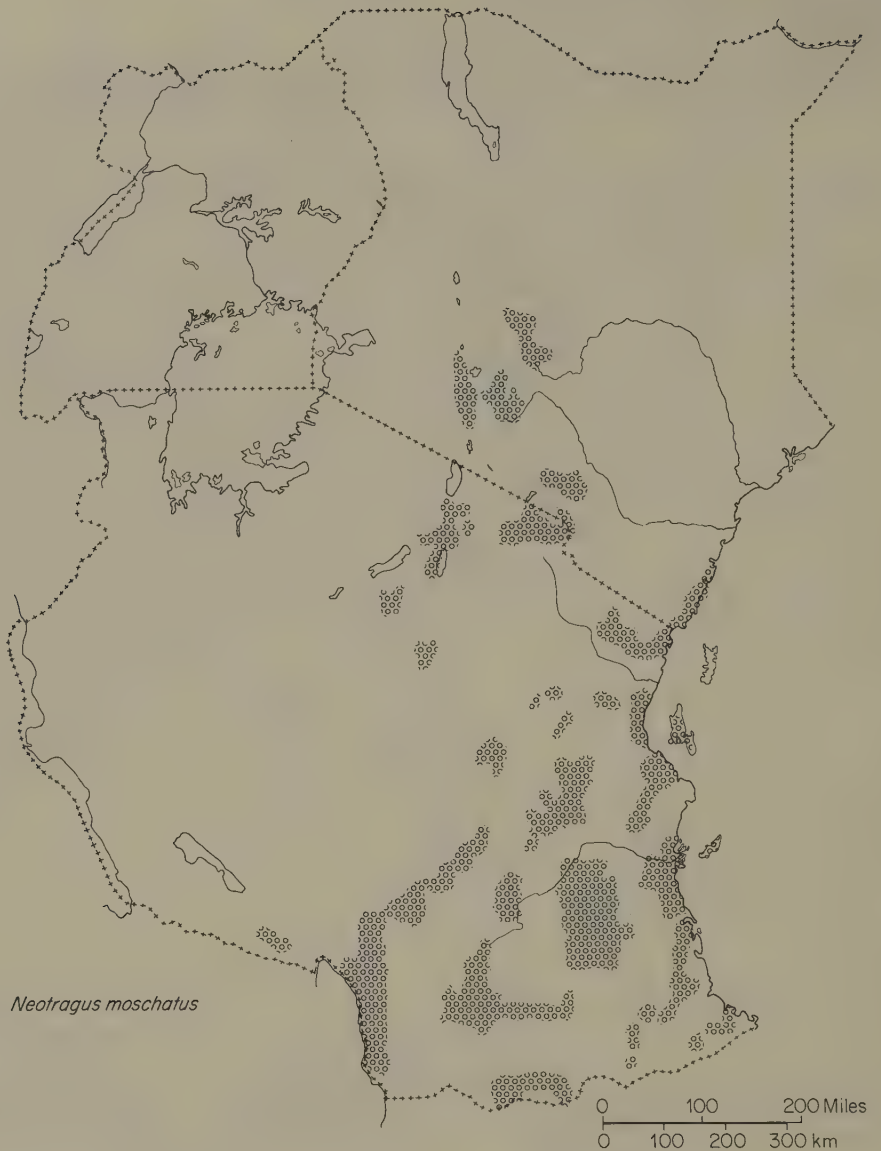
Suni

(*Neotragus moschatus*)

The suni is a dark brown, somewhat freckled little antelope. When in the forest two characteristics stand out—one is the constantly flickering tail, the other is the rather transparent pink-lined ears, which have a peculiar luminosity when the sunlight strikes through them. Two white chevrons mark the throat.

The male's horns although short are sharply annulated along most of their length and only the tip is smooth. The male is also distinguished by preorbital glands that are, in relation to its size, the largest of any ungulate. When they are at their most active, the swollen glands model the form of the face and give it an unmistakable shape. Another characteristic of the species is the short-haired area of skin surrounding the eye, from which several long vibrissae emerge; above the eye this area is demarcated from the longer hair of the forehead by dark "eyebrows".





The suni lives in coastal forests and thickets from the Somali border to Zululand. Its range extends inland as far as the eastern Rift wherever there is thick undergrowth and suni are known from mountain forests as high as 2,700 m. However the suni is unevenly distributed, being relatively scarce in cedar and other high altitude forests and commonest in the broken forests skirting foothills of the more easterly mountain massifs. Even within these forests they may be locally more abundant where the undergrowth thickens along the margins and watercourses.

The suni is not a very specialized plant-feeder, but the following are some representative food plants eaten by suni on West Kilimanjaro (collected by P. Fox); *Crotalaria kenyanensis*, *Jesticia* spp. *Achyranthes aspera*, *Commelina benghalensis*, *Toddalia asiatica*, *Leucas mollis*, *Senecio sarmenosus*, *Microglossa* sp. *Pavonia* sp., *Glycine wightii*, *Clematis hirsuta*, *Acalypha robusta*. In addition to these listed above, most of which are eaten directly

off the plant, they favour *Fleurya* and *Ipomoea* when they are wilted and also various dry fallen tree leaves. They are especially fond of the leaves and shoots of *Nuxia congesta*, which is a staple of the Colobus in this area; the suni picking up the fragments dropped by the monkeys as they feed in the canopy. They also eat charcoal. From the drier coastal habitats in Zululand, Heinichen (1972) lists *Acacia*, *Grewia*, *Strychnos*, *Cissus rotundifolius*, *Xeromphis*, *Wightia*, *Davyalis*, *Gardenia cornuta* and *Sapium* as well as termitary mushrooms (see Vol. I, pp: 43—44). *Digitaria* spp. and other grasses have been recorded and they are also reputed to uncover the thickened roots of certain herbs in order to eat them.

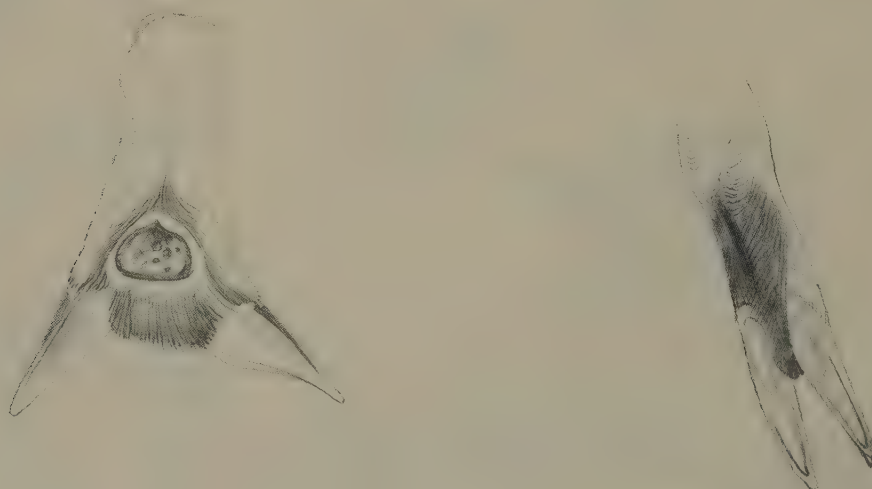


Suni wrench up their food and prefer to eat with the head raised and alert; larger leaves and branches are shaken vigorously. Suni will feed at any time of the day but they generally lie up and sit tight when it is hot in the middle of the day, and they are especially active after rain or mist. Fox (personal communication) watching captives in a paddock found them active at night until 10 p.m. and again in the early morning from 4 a.m. onwards. They have relatively short feeding spells of 15–90 minutes with longer spells in between for ruminating and resting, and they engage in much self grooming, licking and scratching, the male paying considerable attention to his own genitalia. I noticed that a suni resting alone would often fluff its hair out, whereas a pair lying side by side and occasionally licking one another tended to have their sleek, shiny fur lying flat against the body. The male would frequently lick the female's neck, legs and genital area in between grooming his own.

If disturbed they flee in a very fast zig-zag, sometimes uttering a wheezing double screech, after a short rush the animal stops and sniffs. It will often freeze in total immobility, which for an observer is often sustained for painfully long periods of time. When only very mildly disturbed they may creep away with the head low, walking on the tips of their toes. This species has never been seen to “pronk” or “stot”.

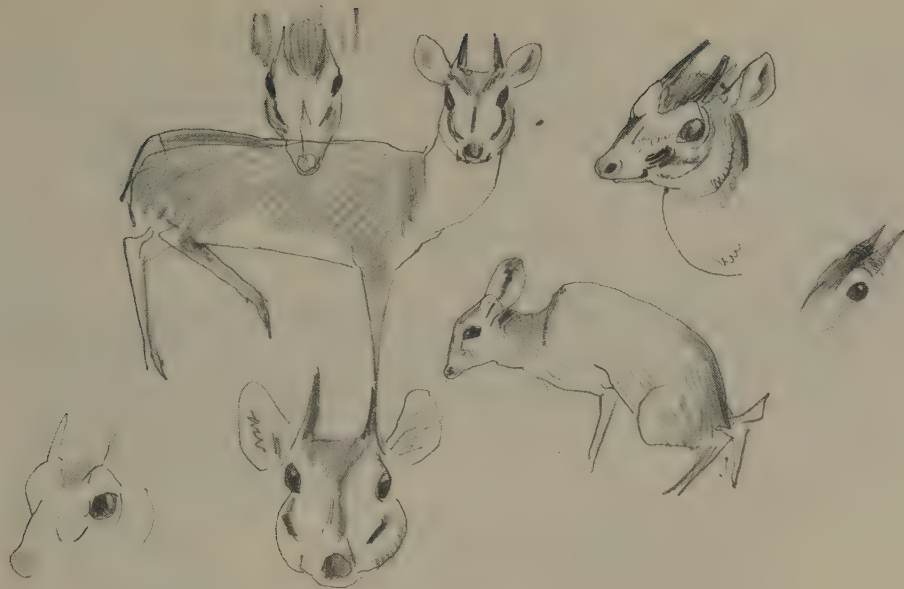
They have favourite tangles in which they lie up and invariably make for these when disturbed while feeding, always using the same scarcely perceptible pathways. I have watched a young one emerging from shelter and seeking its mother: it followed a path with its head held low and much sniffing.

Suni hind foot splayed to expose pedal gland—note fan of hairs. Black fur coincides with area in which scent diffuses.



Olfactory clues are obviously of the greatest importance to this species, which has large glands between the digits, highly developed preorbital glands and a generally strong body odour, which is memorable to anyone who has tried to keep them in the house.

In forests where the suni is numerous, males are generally spaced about 400 m apart. In the course of netting operations, Morgan Davies (personal communication) estimated territories of approximately three hectares and



he encountered about 50% in pairs and the remainder in groups with up to four females, but never more than one male in a group. The largest group seen in the wild consisted of eight, but this may have been a temporary amalgamation of two groups as two males were thought to be present. In a paddock of one hectare two males established territories centering on clumps of thicker vegetation; as many as six females accompanied them at one time, but when I was observing them four females were sharing the paddock. It was evident that each male associated more closely with one female, near which he always rested. These pairs were of long-standing and the two surplus females were much more loosely associated with the males. If disturbed, all six suni would take refuge in one or other of the thickets in the male territories. On at least four occasions, a male came back from his territory to the favourite female, licked her and then walked home, whereupon she followed, giving every appearance of having been "fetched". In contrast to this behaviour after a scare, food attracted the sunis out of their refuges to feed together, after which the females were the first to return to the thickets. Males are usually the first to break cover when disturbed, juveniles last, and fawns sit tightest of all. In the course of frequent scares (which can even be set off by a chorus from Colobus monkeys), individuals may encounter neighbours and I saw the female belonging to one male approach the other male in the paddock and they briefly touched noses, apparently sniffing at one another's facial glands before parting. A male venturing back into his area after such a scare grated his horn on overhead branches and marked twigs with his glands; meanwhile he lashed his tail with exceptional vigour.

Throughout a suni's territory there is a scattering of gland deposits on the tips of any convenient twigs (6—25 cm above the ground), beside the faintly defined pathways which are, presumably, also well scented by the pedal glands. On the boundaries there are dung deposits which are added to by all the suni in a group; however, P. Fox (personal communication) saw suni in an all-male captive group make individual as well as communal



dung deposits. The dung ceremony follows the usual neotragine sequence of urination followed by defaecation.

In the confined groups mentioned earlier I noticed a marked increase in the frequency of tail wagging as a male entered his neighbour's area. These two males had been established for nearly two years and on two occasions another male was put in the paddock; in each case the stranger was chased relentlessly for two days, after which he was reported to have died without obvious wounds. Three female additions were accepted without trouble. When chasing an introduced male, the aggressor champs his jaws continuously and strikes glancing blows with the forehead (not the horn tips) against the jinking escapee's rump or flanks. However, a male suni killed a young male dik-dik that had been put into his pen with repeated stabs of his horns in the dik-dik's abdomen and throat.

Fox watched two males anticipating a fight; they energetically grated their rasp-like horns on a branch, meanwhile licking their own facial glands with the long tongue. Once again the close association of the gland with horning is interesting. Threatening tilts of the head and jabs with the horns are usually dodged, in which case a fight seldom develops, but if the opponent retreats the attack may be pressed home. On the impact of the horns, each animal drops on its knees and jabs, all the while champing the jaws. Fox's hand-reared male suni directed horn threats towards people in its pen; this was probably a product of being imprinted on human beings. When the same animal was picked up it made no attempt to use its horns but kicked vigorously and bit, drawing the lips back and trying to chew with the cheek teeth. On two occasions I saw a female threaten another over food with her head lowered and ears back. I was struck by how the black marks on the top of the ears resembled horns when in this position.

When a female is being followed by a male her tail is raised and wagged horizontally, whereas the normal wag is limp. The female appears to have a post-partum oestrus and a female is closely attended by a male for about 12 hours after parturition.



The preliminaries of courtship bring the male to the side of the female; pressing his chest into her flank, he strokes her belly or ribcage with one foreleg. I was interested to find that a very young suni struck out with his foreleg when pressed firmly on the chest, suggesting that the *laufs Schlag* reflex is built into the male before maturity.

Although they were probably fertile well before the age of one year, Fox's captive males only acquired fully adult characteristics at the age of 14 months, at which time the facial glands swelled visibly and the animals became particularly sleek. The latter characteristic lasts about two months and Fox thinks it may reappear cyclically but he has not seen any noticeable fluctuations in the size of facial glands. Breeding is known to occur in most months of the year but there is probably a birth peak between November and February in northern Tanzania (Morgan Davies, personal communication).

The gestation period is believed to be about 180 days (Izard and Unfleet, 1971) and females are sexually mature at the age of about six months. Fox watched a female give birth in captivity, lying on her side and uttering some high-pitched bleats before the fawn came out. The placenta, which emerged 15 minutes later, was eaten.

The fawn hides in thick vegetation and emerges in response to the mother's soft bleat. The young makes a call that sounds like two marbles ground together, so quiet that it is inaudible to the human ear at a distance of about one metre; it may have ultrasonic components. The fawn finds the nipple with strong combing and champing movements and suckles strongly but very briefly; it can only suck through the very front of the mouth.



Almost any movement in the fawn's vicinity is greeted with little sniff-snorts, but an alarm sends the fawn in a fast skulking run straight for cover with its ears back. As it gets older it emerges more frequently to seek its mother and I saw a hungry captive rapidly alternating the impulse to come out with that of hiding itself. The mother stimulates the fawn to excrete by licking the genital area and swallows its excreta. Once weaning has begun this pattern alters as the fawn, after raising the rump very high to be licked, then brings the haunches down sharply so that its pellets fall to the ground. This may occur at the midden. I once witnessed a curious incident in a pen, where a subadult male bushbuck deliberately licked the anal area of a three-day-old suni.

Both facial and pedal glands of the fawn become active soon after birth and, even at the hiding stage, the animal possesses a strong odour. There is a dense growth of very fine guard hairs around the front of the preorbital gland. A tame young male evaded attempts to touch this area, suggesting that its stimulation is unpleasant at this stage. Like other neotragines, the lactation period is short and the young start nibbling at the vegetation within a few days of birth.

Hoppe, Fox and Morgan Davies kept these animals in pens with other antelopes, with which they lived amicably, except that young dik-diks and bush duikers smaller than adult suni tended to be chased and, in one instance,

a newly introduced subadult male dik-dik was actually killed by the dominant male suni. On the other hand, they respect adults of this species and I saw a female suni near a hidden duiker-fawn hastily make way when the mother approached. Suni seem to be troubled by few flies, even when neighbouring bushbuck and duikers are being severely pestered, which suggests their scent may be repellent to these insects.

Suni are very vulnerable to drives with dogs and netting and even more to snares and traps baited with their species' dung. However, they are less widely eaten than they were, having once been sold alive and maimed in coastal markets, so that Muslims could perform *hallal*. At present this species is widespread and numerous in the thickets and forests of the coastal belt and it is not in any danger of extinction.





**Sharpe's
Grysbok**
(*Raphicerus
sharpei*)

Family

Bovidae

Order

Artiodactyla

Local names

Kavulya (Kinyamwezi), Kikururu
(Kiyao, Kingoni, Kimagindo).

Measurements
head and body

61—75 cm

height

45—60 cm

tail

5—7 cm

weight

7.5—11.5 kg

horns

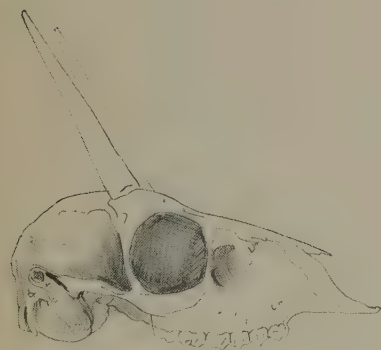
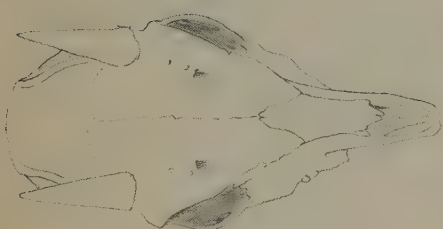
3—10 cm

Sharpe's Grysbok (*Raphicerus sharpei*)

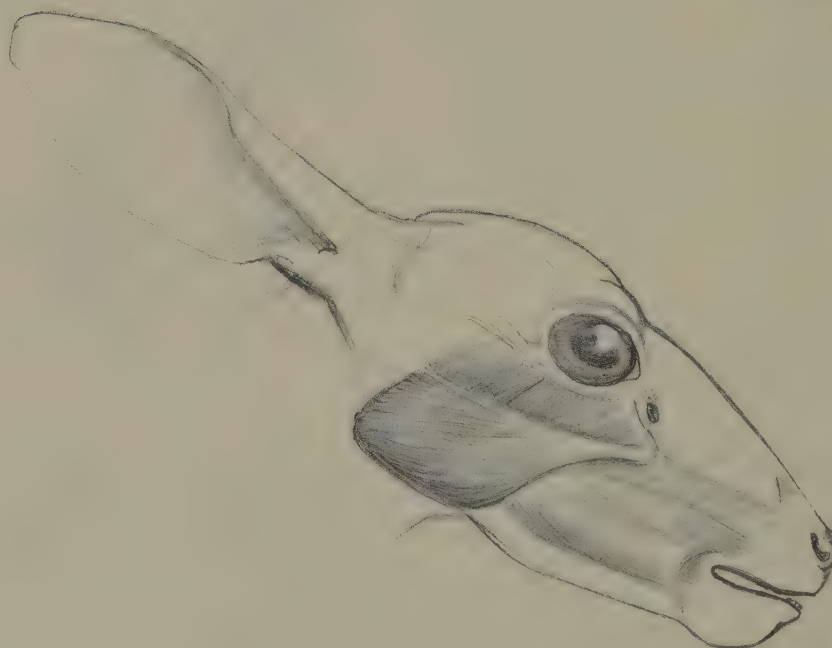
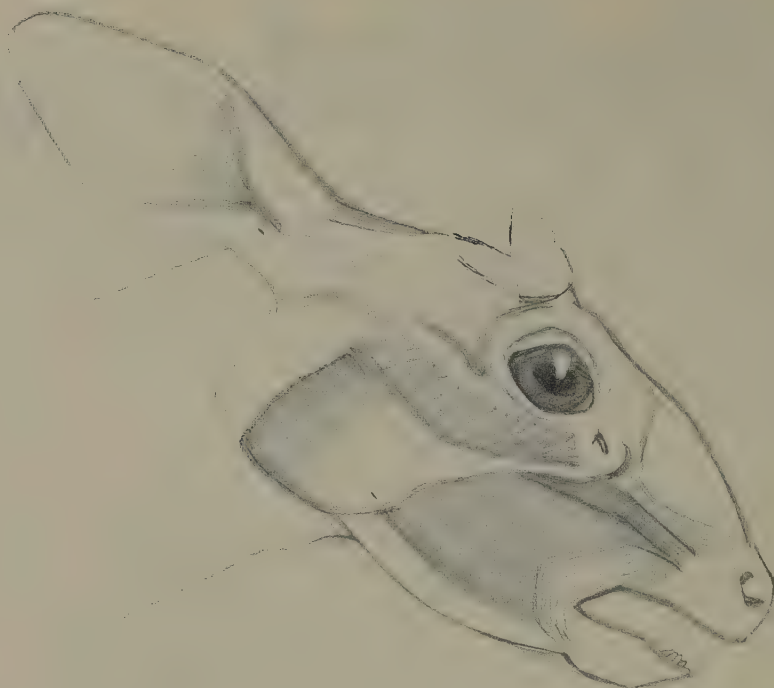


The inclusion of this species in the same genus as the steinbuck, *Raphicerus campestris*, is more a matter of convention and convenience than an accurate reflection of its closest affinities, and the grysbok has given problems to taxonomists from an early date. Gray (1843) allocated it to *Oreotragus* and Sclater (1895) put it in *Neotragus* (both of which have some common features, particularly in the skull), Thomas and Schwann (1906), Pocock (1910) and Roberts (1951) got round the difficulty by means of a separate genus, *Nototragus*.

The reasons for the taxonomic uncertainty lie in the grysbok's intermediate characteristics. The body form and the skull have a hint of that compactness and stockiness typical of the klipspringer, *Oreotragus*; the proportions of the body and skull, the less prominent orbits and eyes and the skulking gait are reminiscent of *Neotragus*, while the polished, ridgeless horns and the small pre-orbital glands seem to put it closest to *Raphicerus campestris*. The Cape grysbok, *Raphicerus melanotis*, links Sharpe's grysbok with the last species justifying the retention of the common genus.

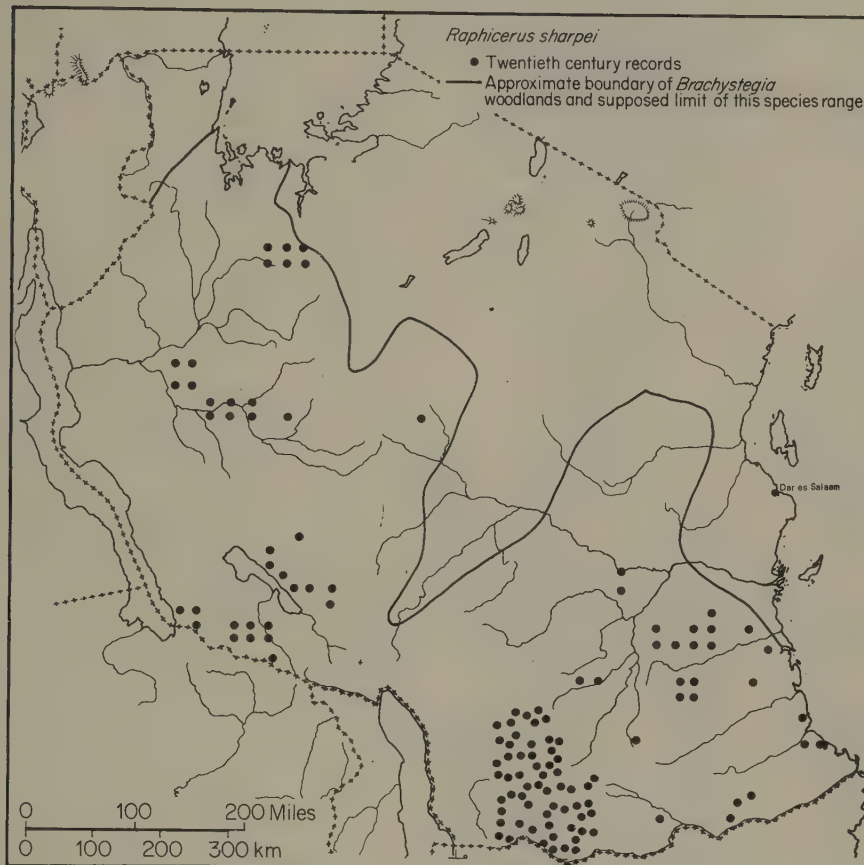


Above: *Raphicerus sharpei*.
Below: *Raphicerus campestris*.



Nonetheless the differences between *R. sharpei* and *R. campestris* are conspicuous. The ear of *R. sharpei* is about 20 mm shorter and the eye, which is set within a more streamlined skull, is not only physically less prominent but its shape is obliterated by the grizzled pattern that surrounds it, revealing the greater importance of concealment for this species. The hindquarters are also less conspicuous. However, the greatest difference concerns the mouth and teeth: where *R. campestris* has a small mouth, long muzzle and moderately developed teeth, *R. sharpei* has a large mouth in a short muzzle and remarkably robust teeth.

Very little is known in detail about the grysbok as it is almost entirely nocturnal, but it would seem that mature plant material plays a larger part in its diet and that, given the relative aridity of its habitat, its dry season fodder is likely to be tough. The grysbok lives in a very much more heavily vegetated habitat and fruit pods and roots are eaten more by this species than by *R. campestris*.



Generally scarce, the grysbok favours areas within the woodland zone where there is low thicket or secondary growth, and this type of vegetation is most commonly found after cultivation has been abandoned or elephants have been busy, or along the base of stony outcrops, where the fire cannot burn off the undergrowth. It favours the foothills of broken country in preference to the hilltops and the valleys. *Acacia*, *Albizzia*, *Boscia*, *Commiphora*, *Grewia* and *Strychnos* are common trees that supply shelter and browse (see Vol. I, pp. 32—33). Grysbok feed at night but, in the rains and when the sky is overcast, are occasionally active during the day, mostly in the early mornings and evenings. Captives have confirmed this activity pattern by sleeping all day and wandering about all night.

The cryptic colouring mentioned earlier and also the animal's ability to lie close are evidently very effective, because grysbok are seen less frequently than are their dung middens and tracks. When they are put up they have a peculiarly smooth motion with the head held low as they make for another nearby thicket where they can again drop out of sight. If very



Total range of
Raphicerus sharpei



frightened, a grysbok may zig-zag through the vegetation but it seldom runs very far. It has been reported to hide in aardvark holes (Smithers, 1966).

The grysbok's attachment to a place is one aspect of its territorialism. Said to be solitary, except during the breeding season, further enquiry suggests that a loosely connected pair share a territory throughout the year. Roberts (1951) described seeing at night what might have been territorial males taking up positions near heaps of droppings in spots that were close to or amongst the scrub. When alarmed during daylight, he remarked on the short stamping hops with which these animals begin their flight before darting off through the tangles.

The sexual behaviour of this species has not been recorded, but the young are not infrequently found when they emerge from their hiding places at a disturbance. Kerr and Wilson (1967) found evidence of breeding throughout the year. In the Southern Highlands there is thought to be a birth peak in January and Ionides (personal communication) reported births at the beginning of the rains (November) in the southern province



of Tanzania. Smithers (1966) reported births in Central Africa in the early summer months. The young are distinguished by a black patch between the ears which fades with age.

The fondness of this species for secondary growth brings it into close contact with the shifting cultivators of the woodland zone and it is regarded a nuisance eating cowpeas and gnawing millet and beans. It is vulnerable to hunting with dogs but in one of its main strongholds, north of Lake Rukwa, it is taboo as food and the local people will not eat it.

In East Africa Sharpe's grysbok may be the nearest approximation we have to the archetypal antelope. It certainly merits a detailed comparative study.





Steinbuck
(*Raphicerus*
***campestris*)**

Family

Bovidae

Order

Artiodactyla

Local names

Funu, Isha, Dondoro (Kiswahili),
Enkaakuluo, Olbwansas (Masai), Kabulwa
(Kamba).

Steinbuck (*Raphicerus campestris*)

Race

Raphicerus campestris neumanni

Measurements head and body

80 (70—95) cm

height

50 (45—60) cm

tail

4—6 cm

weight

10.5 (7—16) kg

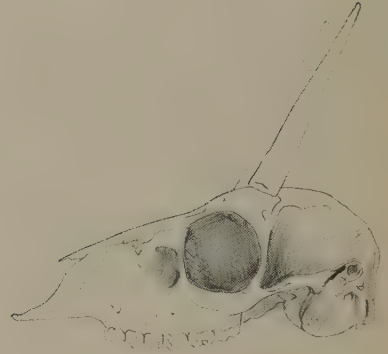
horns

9—19 cm

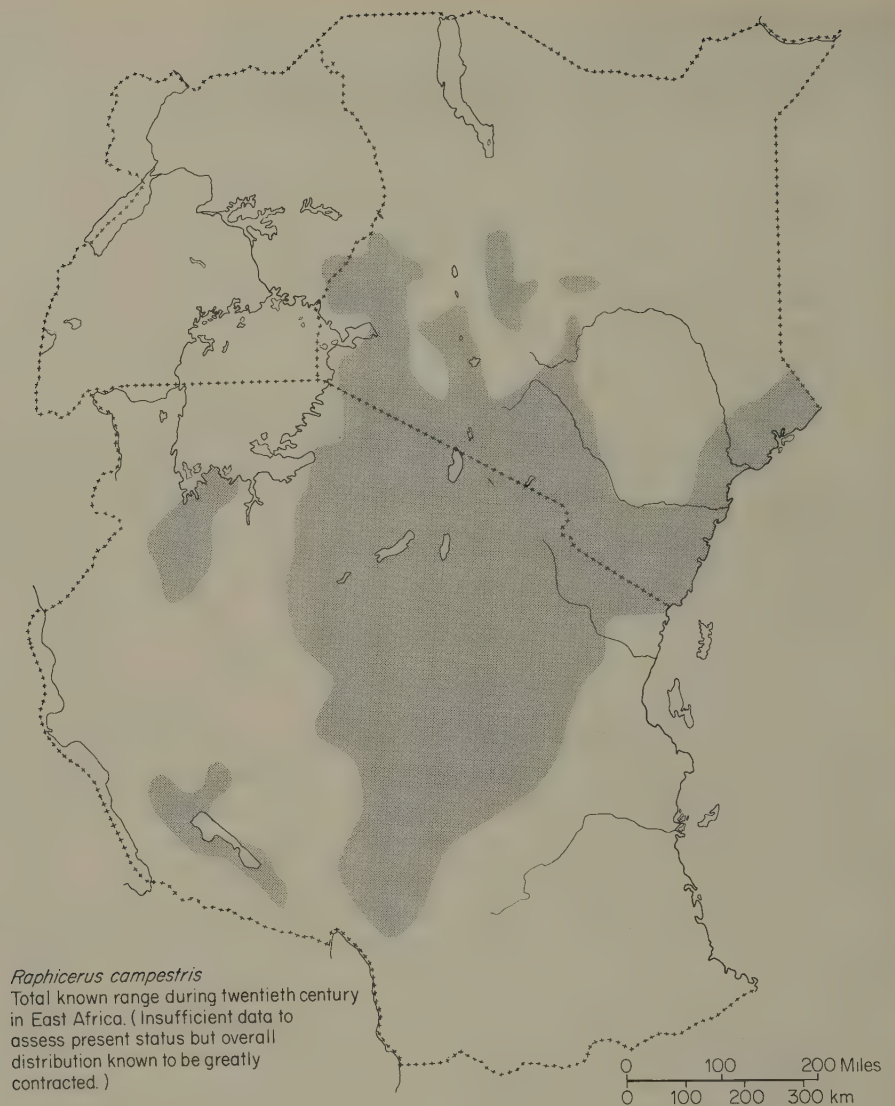
More slender than a bush duiker, less so than an oribi, the steinbuck is often mistaken for one or the other. Its very large white-lined ears, reddish-fawn coat and white throat and belly are characteristic, as are the prominent buttocks, shiny black nose and, in the males, very upright polished spike horns. A peculiarity of the male skull is the heavily granulated texture on the top of the skull, which is presumably a protective adaptation against damage in horn fights but might also signify an archaic condition.

This animal is essentially an eastern and southern savanna species, its range broadly bisected by the *miombo* woodlands, in which it is either very rare or absent altogether. Although there are areas of overlap, the grysbok, *R. sharpei*, seems to replace it in the woodlands. The ecological exclusion is very interesting because over most of its southern range observers have stressed that the steinbuck is an animal of open plains, never found in wooded or broken country. However, in Kenya they are abundant on stony well-wooded hills in Ukambani and in *Acacia* groves in Laikipia. As *R. sharpei* is absent from Kenya, *R. campestris* might occupy a wider ecological zone here than in the south. They live in quite a wide range of lightly wooded grasslands from sea level up to 4,750 m, the main characteristic of their habitat is that the woody growth is in decline. A marked increase in steinbuck was noted after the bush had been cleared for the Kongwa groundnut scheme and similar increases are thought to have occurred in former bushland opened up by cultivation, road building and by elephants and other ungulates.

The steinbuck seems to be the beneficiary of these conditions because for many years there remains an abundance of hardy scrub, the growth of which is regularly cut back to ground level by slashing, trampling, bulldozing or browsing so that new shoots are constantly reappearing.



Total range of
Raphicerus campestris



The steinbuck browses at or near ground level; furthermore it is adept at scraping up the roots and tubers of some plants with its sharp little hooves. An inventory of food plants from the Kruger Park (Pienaar, 1963) revealed that they favoured the shoots of the dominant bushland trees and shrubs, namely *Acacia*, *Combretum*, *Colophospermum* and even *Euphorbia*. The fruits of *Sclerocarya* and *Balanites* and the leaves of *Strychnos* and *Adenium* were also recorded.

In an examination of twenty-one stomachs collected in Central Kenya, Hofmann (1973) noted marked seasonal changes in diet. The proportion of grasses increased to almost two-thirds during the early rains or after burns, whereas during the dry season the staple of low herbaceous plants such as *Commelina* and *Sida* was augmented by large numbers of *Acacia* leaves and pods. Seeds of *Cynodon* and other grasses were also found in large numbers, systematically stripped off their stems. Hofmann classified steinbuck as a mixed feeder with a preference for rich, easily digestible material, including young grass.

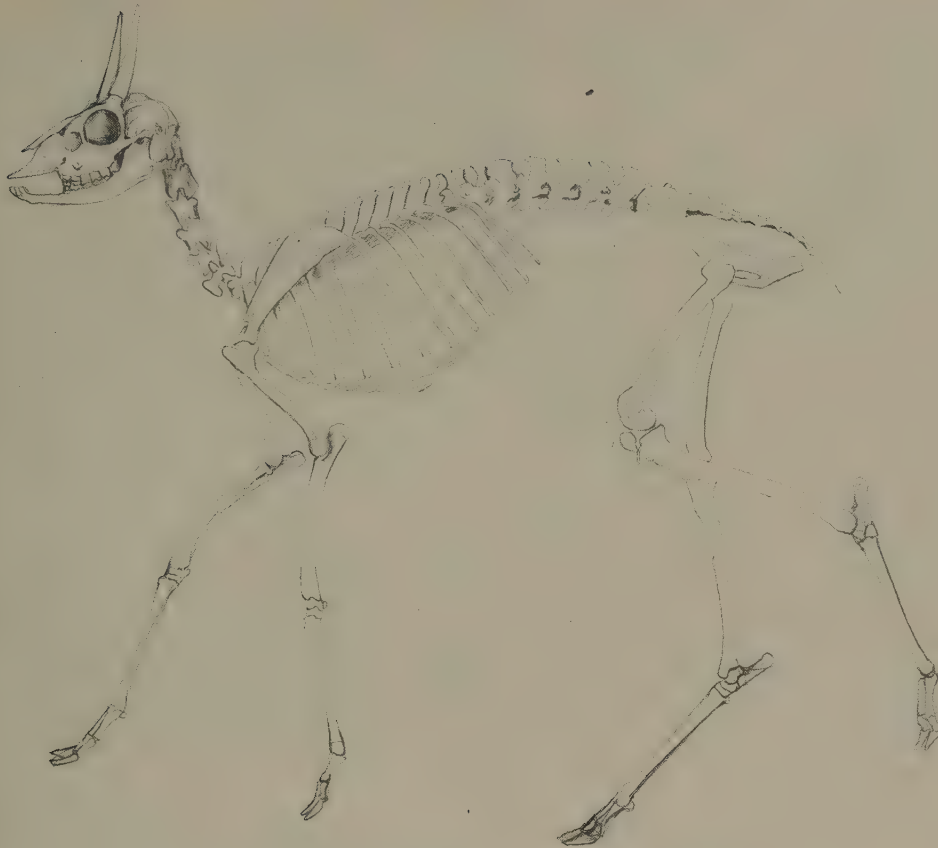


As was stressed in the discussion of neotragines, this species belongs to a transitional and unstable ecological zone, often in a very dry climate. For instance, in the Kalahari desert steinbuck live 80 km from water and can evidently manage without it, an ability probably helped by their largely nocturnal habits.

In spite of being rather conspicuous, the steinbuck very often lies down and freezes at the sight of a man or predator, retracting its enormous white-haired ears so strongly that it looks earless. It watches an approach attentively and flees if danger draws too close. Derived from bush and forest-dwelling stock, this neotragine still employs a behaviour pattern that sometimes seems inappropriate. Nonetheless, it has elaborated the typical neotragine zig-zag flight behaviour and also acquired speed and mobility that serve it well in exposed habitats. Percival's (1928) account of a hunt with fox hounds illustrated this:



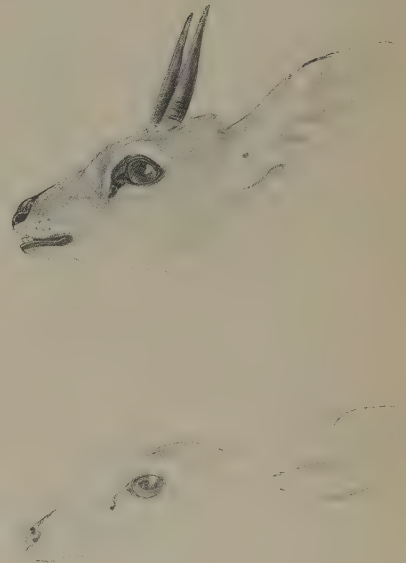
"A steibuck came flying down the hill from the direction in which the hounds had gone. . . . I saw it 'wrench' sharp to one side, run perhaps 50 yards and then make another sharp turn to resume its original course; again it did the same thing, this time to lie down in some long grass . . . as soon as the pack came near he got up, fresh as possible, and went away straight for Mt Suswa, five miles off. When he passed out of sight he was still going strong."



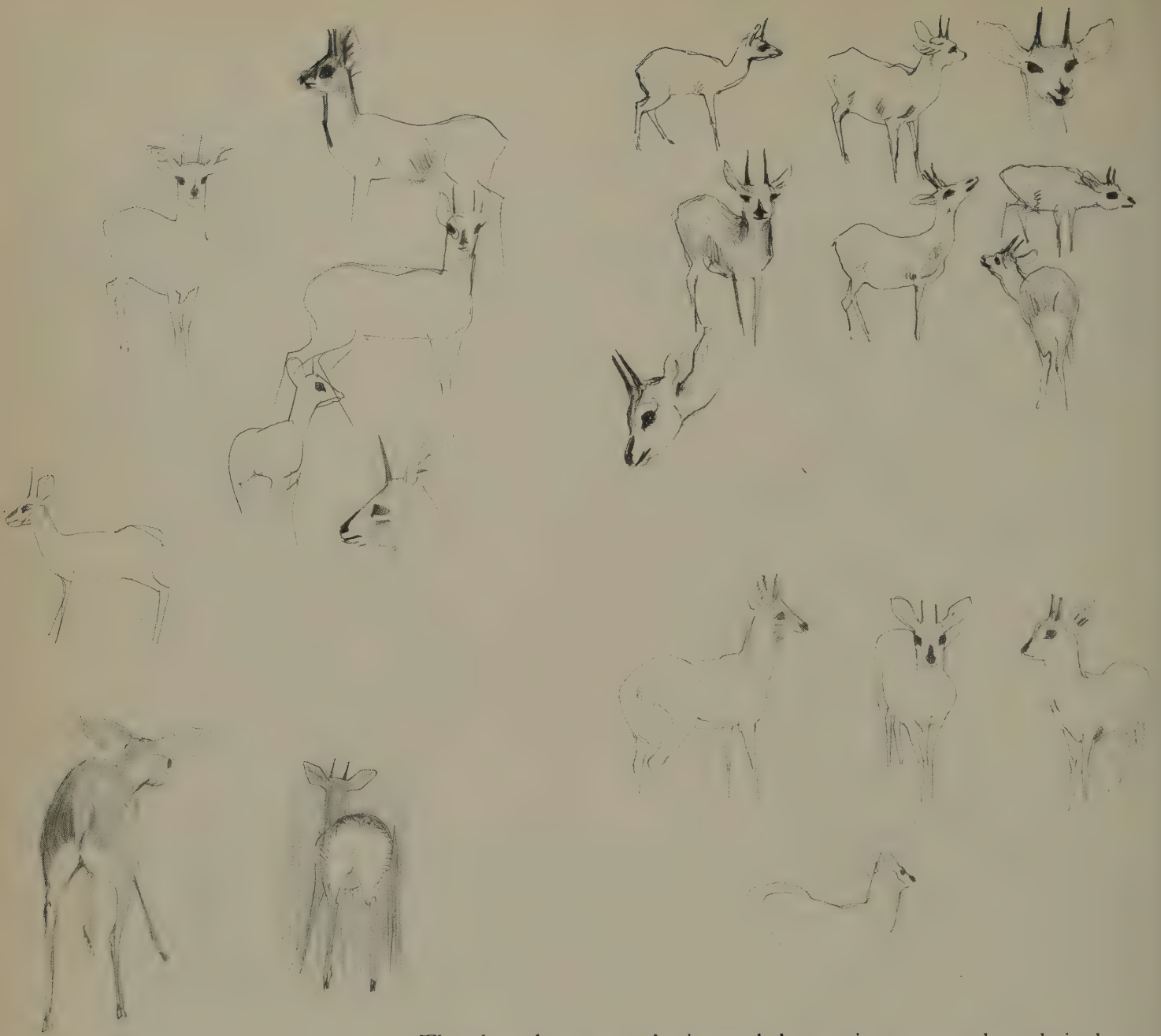
The same author mentioned that the young may be hidden in holes and he described a wounded steinbuck trying to escape him by going down a hole. Smithers (1971) has actually photographed a wounded steinbuck in a burrow. The only dark corners in the wide plains, aardvark holes are not impossible refuges for an antelope. Captive fawns show the classic neotragine escape mechanism of running to a cupboard, chimney or dark corner and equivalent shelters are certainly hard to come by in some of the more open steinbuck habitats.

Even in favourable localities, this species seems to be very unevenly distributed and, although it is possible to see groups grazing near one another, including several males, it is much commoner to encounter single animals or pairs that are well spaced out from their neighbours.

The sexes normally show an even ratio. Sedentary and territorial behaviour and the spacing out of animals in pairs is borne out by Hofmann's (1973) observation that in eight out of ten cases a female was seen not to move more than 300 m from a male and that one identifiable male was seen feeding in the same locality for five years. Other observers have estimated home ranges of four or five hectares. Hofmann estimated that territories might range up to one square kilometre in extent. The insignificant development of the facial glands may be correlated with the abandonment of a small, well-known and intensively used territory in favour of a larger range in which food can be sought over a wider area.



Sexual dimorphism in steinbuck.



They have been seen chasing and threatening one another; their dung piles also give evidence of a neotragine-type territorial system (both sexes scrape in between excreting). Kerr (personal communication) has seen as many as 32 together in the Kedong Valley and it would be very interesting to know what ecological pressures could be responsible for such an unusual build-up of numbers. I have not seen this species marking with its moderately developed preorbital glands, nor am I aware that this is as common as it is in the other neotragines. This point might be of some significance in relation to the size of territories and the method of demarcation.

The horns are quite formidable spikes, and Chalmers (1963) and Fox (personal communication) have reported captives and hand-reared males attacking animals as big as an eland and an ostrich, running alongside and stabbing with a sideways yank of the head, behaviour that is apparently triggered off by the female's oestrus.

In contrast with this use of horns in territorial behaviour, they make no effort to use their horns when grabbed, kicking out instead with their sharp hooves.

Known predators are cheetah, wild dogs, caracal, jackals and hyaenas.

Steinbuck breed throughout the year but are thought to have at least one and probably two birth peaks in southern Africa. However, the evidence is rather contradictory. Wilson and Kerr (1969) recorded a birth peak in November—December in Rhodesia; Bigalke (1963a) thought there was one peak at the end of the wet season and another at the end of the dry, while Smithers (1966) says that August and March are the peak months in South-Central Africa. Chalmers recorded a consistent birth interval of eight months in the same female but Bigalke records a range of between nine and five-and-a-half months. There is evidence that an early post-partum oestrus may be common (Mentis, 1972).

Gestation is 168—177 days and, according to Chalmers, courtship in captivity is rather abbreviated but is preceded by face nibbling. Wild steinbuck have been seen to perform the leg-kicking or *laufschlag* movement.

A young one has been observed being born after a protracted labour of seven hours. The young weighs about one kilogramme at birth and sucks within five minutes of birth. It nibbles at grass within two weeks and is weaned by three months. It may be sexually mature between six and nine months and Bigalke (1963) records a female calving at the age of one year.





Oribi

(*Ourebia ourebi*)

Races

<i>Ourebia ourebi aequatoria</i>	North Uganda
<i>Ourebia ourebi cottoni</i>	Southwest Kenya to Central Tanzania
<i>Ourebia ourebi haggardi</i>	Kenya Coast
<i>Ourebia ourebi hastata</i>	South of Rufiji River
<i>Ourebia ourebi kenyae</i>	Vicinity of Mt Kenya
<i>Ourebia ourebi masakensis</i>	South Uganda, North-West Tanzania

With legs bent and head low, fawn or russet coat blending with the long grass, a female oribi creeps for cover and crouches with its ears folded and head on ground. Exposed on a nearby ridge, three or four oribi stand in a group with upright ears and alert faces above slender necks. A male, distinguished by its straight spiked horns, canters on long legs with a bouncing rocking-horse gait up to a grassless patch where it sniffs a grass stem then inserts the point into its facial gland, stamps a hindleg and then defaecates ostentatiously.

Many naturalists have been struck by this "duality" of the oribi—on the one hand a solitary, cautious and inconspicuous inhabitant of the moist grassy savannas, on the other a self-advertising and occasionally semi-social member of the open grassland ungulate community.

Some environmental, morphological and behavioural implications of the oribi's peculiar habits and ecology can be touched upon here. Its unique phylogenetic position as a very conservative yet highly specialized antelope was discussed in earlier profiles (p. 23). The contrasts have some correspondence with the annual changes that take place in their surroundings. During the rains, while the grass is long and dense, visibility is cut to a metre or less and animals must rely on scent or hearing; in this closed habitat scent provides the means of charting the geography of an oribi's environment. In the dry season, after the fires have left the animals exposed, scent retains its importance but sight suddenly becomes a primary sense and it is clear that an oribi is alert to every movement of its neighbours and to any suspicion of a predator.

Visual and olfactory signals are closely interrelated for the oribi. Like other small antelopes movements to which the animal is especially responsive tend to be the artefacts of scent-marking—excretory postures, various fluffings and flarings of the buttocks, gland marking, foot stamping and scratching. However, these motions have been very highly ritualized in the oribi and they have been documented in some detail by Monfort and Monfort (1974). For example, a common species-specific action sequence has been identified in which the female repeatedly squats but very often without the emission of urine or dung.

Oribi (*Ourebia ourebi*)

Family Order Local names

Taya (Kiswahili), Lajwar (Lwo), Ensirabo (Luganda, Runyoro), Ndororo (Kikuyu), Amiamu (Ateso), Muche (Lugbara), Ekusogwan (Turkana), Ogunde (Luhya), Darendari (Kiduruma), Ejusi (Masai).

Bovidae
Artiodactyla

Measurements head and body

110 (92—140) cm

height

60 (54—67) cm

tail

6—15 cm

weight

14—19 kg males

15—21 kg females

females average 2 kg

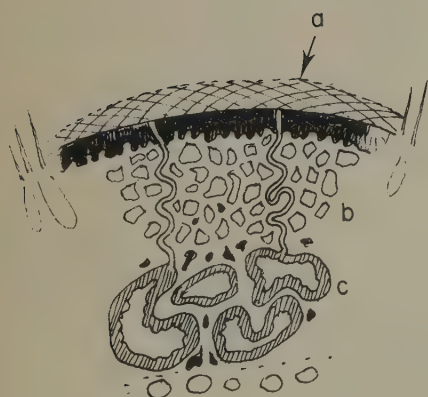
heavier than males

horns

8—19 cm

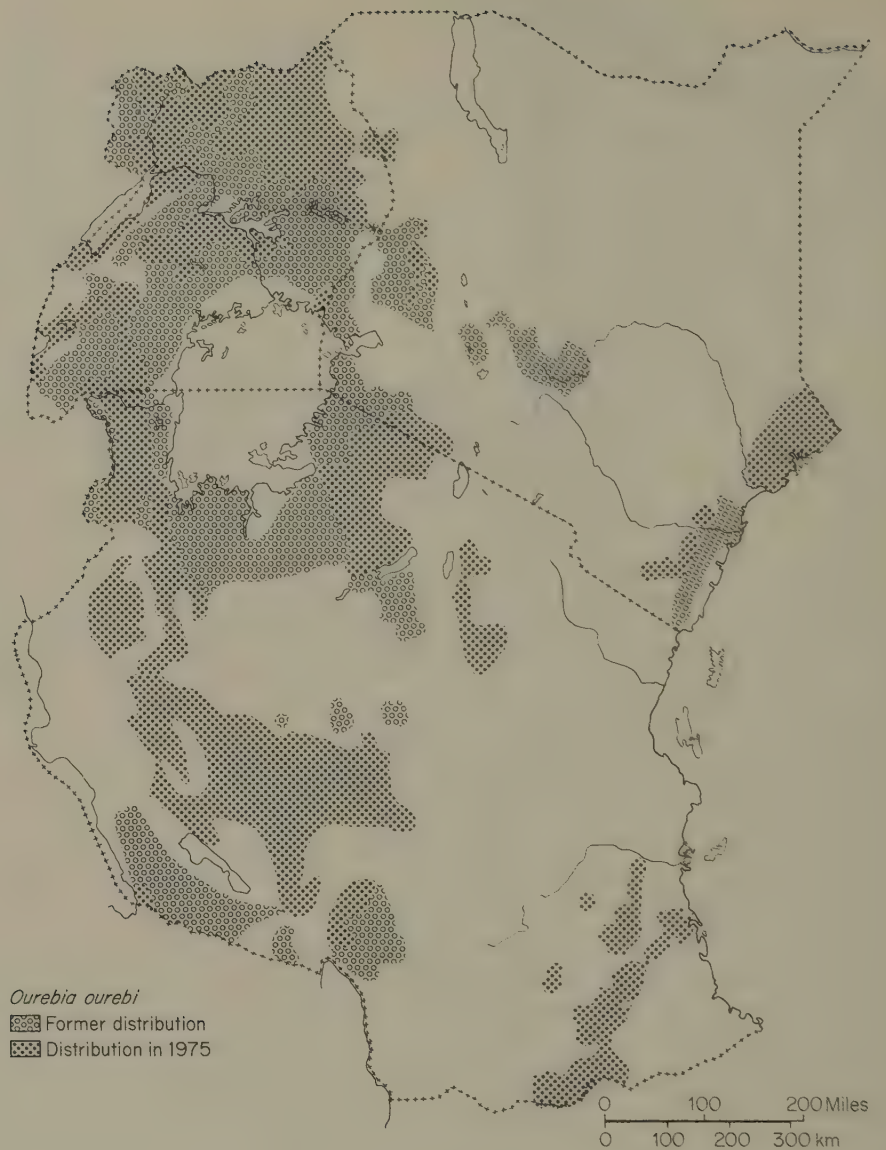
Noting that there are six different sites for scent glands on an oribi's body, Hofmann (1978) has investigated some of these and pointed out how unusually large and active these are for a relatively small antelope.

The preorbital glands not only fill out most of the space between eye and mouth in the male but they actually model the skull. There is considerable variation in the degree to which the fossae for these glands intrude and displace the surrounding architecture of the muzzle, (these differences are predominantly between individuals but it is possible that there may be regional variation as well). The skin is sometimes stretched taut with the swelling of the gland, at which times it exudes quantities of black and transparent secretions which the male transfers to grass stems or to its feet and the ground by repeated scratching with its hindlegs, eventually rubbing away much of the surrounding facial fur. Below the knee on the forelegs there is a carpal brush of very long hair while another pair of shorter brushes occurs at the top of the metatarsus on the hindlegs. Below the hairs of these brushes there are tracts of glandular skin, here sebaceous and apocrine glands make the brushes permanently sticky. Deep inguinal sacs in the groin contain another copious secretion, which is greenish and very greasy. Between the toes there are well developed pedal glands, which exude an oily scent when the hoof is stamped or when the two toes are pressed apart and together again. This lubricates the fur at the top of the cleft. Finally there are circular patches of jet black skin below the ear, the structure of which has been examined by Hofmann (1978). This skin gland is already pronounced at an early age in both sexes. Hofmann found a substratum of blood vessels covered by erectile tissue comparable to that of the penis. The large scent glands embedded in this mass have narrow sinuous ducts and the gland exudes when warm. Hofmann suggested that the arterial system would probably warm up the patch with an appropriate stimulation, especially under the influence of the adrenals. Warmth and expansion within the patch would empty the glands and the secretion would flow to the surface where it vapours as if on a hot plate. Scent particles would then waft out over the grass tops carrying a message to all oribi downwind of the signaller.



The ear gland in oribi. a. black skin (heat storage); b. erectile tissue with vertical ducts (coiled when closed); c. apocrine odoriferous glandular sacs surrounded by arterio-venous system of shunts and throttle veins. Flow of blood filling erectile layer opens ducts and empties gland sacs. Higher temperature evaporates secretion on surface. (After Hofmann, in lit.)





The oribi was the only neotragine antelope classified by Hofmann (1973) as a true grass eater. He found several primitive features in the anatomy of the stomach, notably the omasum, but the rumen and reticulum are typical of a grazer. He observed that oribi consume insignificant amounts of browse, even when this is the most abundant greenstuff available and a subadult captive forced to feed on concentrates lost condition and eventually died. On dissection it appeared that the unnatural diet had damaged and changed the digestive system.

Throughout its patchy but extensive range the oribi is dependent on water and green grass. If adequate moisture is present in the latter, it may dispense with drinking but the oribi's overall distribution is restricted to those wooded grassland types that have a reliable and well-distributed rainfall. Within this climatic regime the edaphic grasslands and marshes

are largely monopolized by the reduncines but, as I pointed out in Volume I (pp. 34—38), the majority of African grasslands and savannas are maintained by fire or heavy grazing pressure. With regard to fire, the oribi appears to be peculiarly well adapted. Where there is an equatorial climatic pattern of two short dry seasons there may be a biannual burn and oribis are one of the few animals that will run towards a grass fire and jump through it. Where males are concerned this may be because their territories hold them so powerfully and it may be for the same reason that they remain on the burnt pasture. Being selective feeders and having modest needs they are the first to find the green grass shoots that appear within a day or two of the fire's passage, long before a large-scale flush attracts herds of larger herbivores. At such times increased exposure to predators may be compensated for by extension of visibility or by the oribi's greater alertness. I have noticed a tendency for them to run or even to crouch flat at greater distances when the ground is bare. Notwithstanding this they still seek out unburnt clumps of taller grass or scrub to rest or shelter in, and oribi are not numerous on open plains that are totally devoid of cover for most of the year.

In the hilly Kagera National Park, Monfort and Monfort (1974) described clusters of oribi territories on flat or gentle slopes that were predominantly grassy. Grass species growing on more exposed and leached soils are shorter, less densely tufted and allow better visibility. The Monforts noted seasonal changes in diet. *Hyparrhenia* and *Themeda* were eaten while green shoots were still available, at other times the less nutritious *Loudetia simplex* was a palatable stand-by. In Kagera, as elsewhere, oribi avoid the gullies and poorly drained hollows. In *Combretum*, *Terminalia*, *Brachystegia* and *Acacia* wooded grasslands they also appear to be commonest in the more open areas of shorter grass, conditions which may be caused by fire, poor soils, by the rapid drainage along watersheds or by trampling and grazing of large animals. It is possible that herds of larger ungulates not only create favourable grazing conditions but, by offering larger, slower, more numerous and often less alert prey to predators, may actually increase the oribi's chances of survival.

In the Akagera National Park, Rwanda, Monfort (1974) recorded the numbers of ungulates seen along a 5 km transect through grassland. Fluctuations in the numbers of oribi, particularly in the burnt sections, had generally some correspondence with the total number of ungulates. Where the grass grows very tall in the wet season and is also without tree cover, the ratio of oribi to other ungulates may become exceptionally high and this is shown in figures published by Spinage and Guinness (1972) for the same park.



Ourebia ourebi

	Open long grassland	Steep hillsides	Open flat plain	Mixed open woodland	Acacia scrub
Total mean numbers of animals	9.4	4.9	67.5	38.7	38.8
Mean numbers of oribi	1.4	0.2	2.7	0.8	0.2

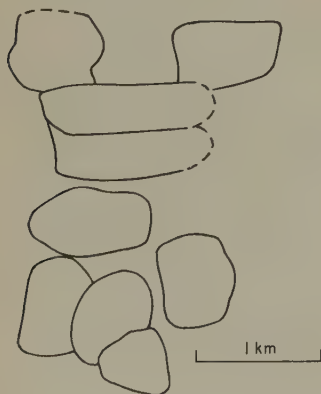
In the Semliki Valley and in those parts of Acholi where there are great kob concentrations there seem to be fewer oribi outside these areas than within them. Likewise in northern Karamoja density is highest where there are large herds of hartebeest and other animals. Where the larger ungulates have been greatly reduced or exterminated, oribi have generally declined or disappeared as well. For example, oribi used to be numerous from Embu westward to Elgon wherever there were open grasslands and they belonged to grazing communities which included hartebeest, buffaloes and zebras (plus topi and kob in the West). All this area is now under cultivation or has been turned over to domestic stock. It is perhaps to be expected that a conspicuous and highly territorial species should have been shot and snared, particularly in densely settled localities. This species is vulnerable to hunting with dogs, and Thompson (1973) recorded nine reports of oribi increasing on Rhodesian farms where dogs were controlled. Also 19 observers cited jackals as predators, and oribi may be susceptible to smaller carnivores after the large wild ungulates have gone. It is interesting to note that oribi continued to be common on some intensively managed farms in Trans-Nzoia and Uasin Gishu until very recently. Possibly they benefited as much from the farmers' control of predators as they did from direct protection, while mown or well grazed leys and paddocks provided ample food.

Oribi occasionally damage field crops such as growing wheat and oats, which resemble their natural diet. Their normal feeding is at ground level, but they have been seen standing on their hindlegs in order to reach seed heads of *Themeda* (Handley, 1951). He remarked on how oribi entered a field at an identical time each day and their activity cycle does appear to be regular for short periods, but I have noticed that the moon and seasonal changes seem to have an influence. Oribi often lie down during the middle of the day but tend to rest longer on hot afternoons and may cease activity during heavy rain. They frequently remain in cover for some time after dawn and the most intensive grazing in the open seems to occur in daylight hours during the early part of the morning and in the evening but they may continue to graze and rest in the open after nightfall and this is particularly noticeable during moonlit nights during the dry season, at which time they tend to be scattered singly or in groups of two or three.

The dense grass growth that is prompted by the rains hides much of their activity at this time but, in long grass areas, there appears to be a tendency for them to gravitate towards areas of shorter grass. Oribi aggregate in groups at this time and on a more regular day by day basis they collect in the vicinity of salt-licks. Indeed major incentives for localized movements may be the oribi's need for shorter grass in the rains and for minerals at all times. The Monforts noted that, in spite of salt-licks of the Kagera area being situated in unfavourable valley bottoms, their siting influenced distribution in that higher densities were consistently recorded in the surrounding country.

On a Kenya ranch with an unusually dense oribi population "territories" were thought to be not more than 3,000 sq. m (Hofmann, 1973) but in the detailed studies in Kagera the Monforts identified and delimited numbers of territories, most of which were in the vicinity of one square

Oribi territories in Akagera (from Monfort and Monfort, 1974).



kilometre. These were occupied by individual males, pairs or families, were defended by the male, and female residents also tended to exclude other females. Territories could be distinguished from larger home ranges in which resources such as mineral licks, emergency refuges and supplementary pastures were shared with neighbouring oribis. Family groups maintained their identity on these neutral grounds even when in close proximity, tolerating approaches up to five or so metres before threatening or chasing. Males commonly prevented other males from coming to the lick and competition was also evident among females. Pair bonds in Kagera were found to be stable and the Monforts recorded pairs remaining together for several years.



Notwithstanding the fact that she shares a territory, a female maintains a high measure of independence. The loose but well-sustained relationship between a male and one or more females appears to gain support from behaviour that is founded on the males' enormous capacity to scent his surroundings.

Marking with the preorbital glands, which is the most immediately perceptible of the male's scent-marking, is predominantly a territorial and sex-restricted activity. The labelling of the land probably benefits both sexes because it familiarizes all the animals living in an area with their home range. However, the Monforts found abundant evidence that female oribi actually *induce* marking behaviour in the males and the *incitation au marquage* sequence that they identified can be anglicized as the "incitation ritual".

They observed that the protracted and highly conspicuous excretory posture of a female invariably stimulates a male, usually the territory holder, to investigate her. As she steps away he marks the nearest stems with each of his face glands, sniffs and then scuffs the females' faeces with his hooves, leaving scent from his pedal glands. Offspring or other members of a family group may interpose their contributions but the ritual usually terminates with the male scuffing and then superimposing his own faeces. However, I have seen the male then mark with his pre-orbitals again after defaecating and with his legs still bent and wide apart.



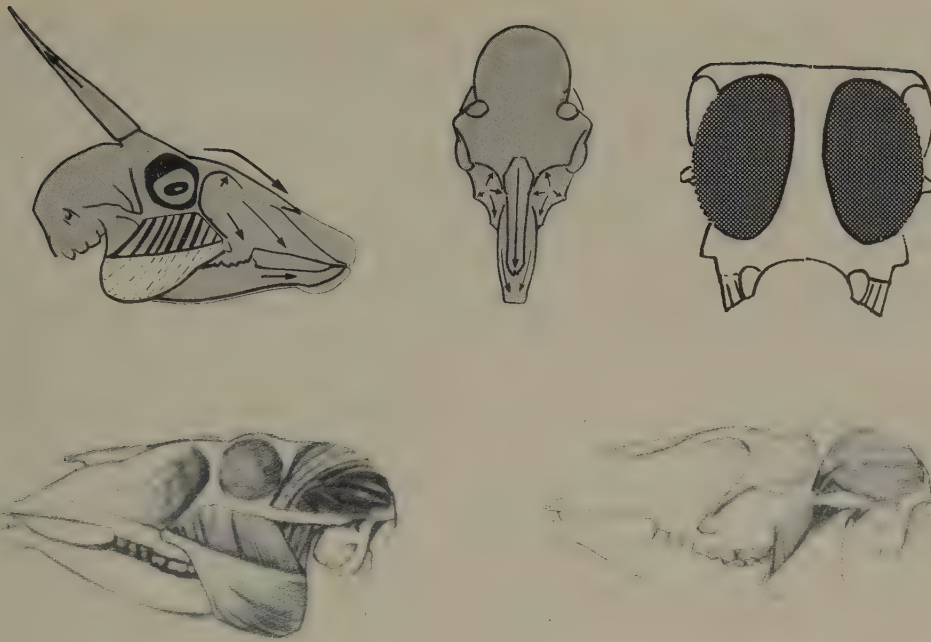
Both males and females may be stimulated by various (mainly olfactory) signals to prefer particular sites for dunging and I have recorded up to 30 identifiably separate and fairly fresh deposits clustered over bare compacted eminences or the sides of eroded termitaries. In areas of high oribi numbers such clusters of dung are common in among the scatter of single deposits (see p. 227) but there are no dense accumulations or latrines as in dik-dik territories. Fresh droppings that are divorced from their authors elicit little or no interest from males; it is the sight of the animals' behaviour that excites them. For the females and young the males' ritualized attempt at obliterating their droppings right under their noses provides a very frequent experience of the scent of his dung, his urine, his facial and other secretions, most of which are also distributed all over the territory, most of them independent of his presence.

The rarity of reproductive opportunities scarcely merits the regularity with which a male samples female condition. There is also little reproductive incentive for the females to provide such a strong stimulus so frequently.

As with "presenting" the performance is ritualized and the advantages are less direct, serving broad social ends rather than immediate sexual ones.

For the females and young there is the important advantage of living more safely within a particular male's territory because the element of subordination in the performance neutralizes any risk of the male attacking them. This is reinforced by repeated sampling and exchange of scent signals all over the territory which thoroughly habituates all participants to one another's presence.

Perhaps even more important, tokens of the male's presence are so frequently imposed upon the senses of the females that their environment becomes unfamiliar without them and it could be the absence of such familiar smells in other territories or areas that induces a female to stay in a particular territory without coercion.



Architecture of the oribi's skull.

It is in the females' voluntary residence within his domain that the male derives his reproductive advantage. Indeed, the Monforts have noted that when herding behaviour does occur it is only when females in a territory are approached from outside by other males. However, once a female was settled on a territory they found she remained there even if the male was killed, after which she would soon become associated with the new territory holder. The Monforts stressed that the lack of familiar smells around an animal gave it inferior status, but they recorded intensive marking and incitation by females on neutral zones such as salt-licks, a response which they attributed to a lack of security in these areas.

Thus the incitation ritual repeatedly familiarizes a very limited number of individuals with territories and perhaps home ranges that are marked out with numerous varied manifestations of a well-known adult male.

The visual and olfactory clues provided by the ritual probably serve to reinforce the links between particular animals and a particular piece of land, condition females to remain within the boundaries of a particular territory and even to exclude alien females.

Behaviours common to most neotragines, notably territorial scent-marking and male monitoring for female oestrus, have combined in the oribi to regulate their social life and dispersion in a unique fashion. Some evolutionary and comparative aspects of this have been discussed in the neotragine profile.

Another ritual that has elaborated neotragine behaviour and involves ostentatious gland-marking follows the close approach of one male to another. A territory holder will assume an aggressive, very erect posture and if the confrontation is near a common boundary both neighbours will mark vigorously, horn vegetation and then retreat without incident. Intruders may be chased or both animals decamp after the territory holder has made his mark. The visual and olfactory message of the ritual apparently

serves to avoid or replace a chase or fight. This activity has been mostly observed in the open but its utility may be even enhanced for close-range encounters during long grass seasons.

After an intruder has been chased, and at any other time when a holder re-enters his territory he marks grasses all the way back to the centre of his land. Marking is actually so frequent in male oribi that there is often no external stimulus or spatial significance that can be discerned, but the Monforts also recorded oribi circulating known boundaries, interspersing their marking of grasses with defaecation and the stereotyped rocking gait.

Biting the top of a grass stem before inserting it into the facial gland is commonly seen where the grass is tall and rank. Gosling (1972b) suggested that older deposits may be removed and eaten in this way, behaviour that has been seen in some other antelopes with facial glands.

Males horn the ground or at tufts of grass rather infrequently, but the Monforts saw horning during boundary confrontations as a response to an opponent that was grass-marking and they regarded it as a displacement activity. They also saw horning after a male had herded females away from a neighbour's territory and when sexually excited but refused by a female.

It is possible that a female's bonds with a particular male may weaken when she is off the territory, in which case an exceptionally vigorous male close to a shared resource might temporarily accumulate a "harem" irrespective of whether he is on or off his territory. I have observed behaviour that might have been indicative of this situation (but without sustained observations of known individuals this can only be speculation).

During one wet season I was able to watch oribi intermittently for some days on a one-and-a-half hectare patch of mown grass. My vantage point, a park building close to a small seasonal spring was also the site of some mineralized earth. During the morning, late afternoon and evening, numbers of oribi, in conventional ones, twos and threes, were attracted by the lick and the grazing but one male seemed to be more residential than the others and he was particularly active in marking and posturing. The area was generally deserted during the latter part of the night and was not visited by oribi until shortly after dawn, then females would sometimes step out of the long grass, look round and then turn back into cover. When the resident male emerged, he ran close to the spring with the high rocking gait, marked and then stood or lay down with head erect, looking this way and that. Only when the male was visible did I see females emerge, but sometimes it was the does and sometimes the buck that took the initiative in joining up. For an entire day this male accompanied four adult does (one with a half-grown young) and the six animals grazed or rested as a compact group until shortly before nightfall when the female with young went off in the long grass, after which the other females appeared to disperse. During the day the male had restricted his own and the females' activities to approximately half of the total area of mown grass, while a mixed group of four horned males, two adult females and a juvenile had grazed over the other half, (the topography of this area and distribution of fresh oribi markings is shown opposite). The resident male interposed himself between this group and the four females and repeatedly marked his boundaries with

on the compound and as aggressive as before. Another free-ranging male that was confined to a grassy island in the Kagera River allowed each of his two male offspring to reach adulthood but before their horns were fully grown pursued them round and round the island and finally killed them. The young would be less easily killed in an unrestricted habitat where there was no obstacle to their leaving the parental home range but there is evidence of numerous other hazards for young males attempting to set up a territory of their own. The self-advertisement that is implicit in territorial behaviour is known to increase the vulnerability of several antelope species to certain types of predators. While inexperience compounds the dangers, the siting of a new territory is also likely to be in an ecologically peripheral location. If older males do remain for many years on the same territory, as several observers have suggested, an old male's survival would itself be testimony to the suitability of his territory as oribi habitat.

An established male defends his territory vigorously and the chances of maintaining his tenancy would probably be increased by his experience in evading danger, whereas the territorial recruit on unfamiliar ground is at a disadvantage on both counts. Survival by old males at the expense of younger mature males is reflected in some counts and shot samples taken by Bindernagel (1968) in Acholi. Of 26 shot adults, 23 of which were classified as old or very old on the basis of heavy tooth wear. In spite of having been a small sample it might indicate that age and experience benefit both sexes. Zoo records indicate that an oribi can live up to 14 years.

Like the steinbuck, oribi fold their ears back on sighting a predator and they often sink down slowly and flatten themselves to the ground. In the open, if forced to break cover, they zig-zag and can run fast, reaching up to 40—50 km per hour, sometimes whistling several short, shrill blasts as they go or hissing as they jump up. If caught or wounded they bleat.

Oribi breed throughout the year but the Monforts noted an intensification of social behaviour during the months of October and January which are relatively dry in Kagera.

In Zambia, Ansell (1963) reported scattered births with a peak between August and November. Thompson (1973) published abundant evidence for a very definite calving peak in Rhodesia, starting in August, reaching its zenith in November and dropping sharply in January, with minimal numbers of young seen between March and July.

The species has a seven-month gestation period and an immediate post-partum oestrus. However it is common for captives not to conceive for several months after giving birth. Bindernagel recorded that 60% of shot females were pregnant and he noted that the oldest age classes had apparently declined in fertility. Oestrus is not the only stimulus for courtship, for a free-ranging male has been seen copulating with a female two months pregnant. This buck showed a periodic swelling of the facial glands which appeared to be correlated with sexual interest in the does irrespective of their oestrus.

Courting male oribi use the legsmack or *laufs Schlag* movement and gentle muzzling or butting. Cade (1966) described how a captive male pushed his head and neck between the female's hindlegs and lifted her hindquarters off the ground. At no time did he see either of the females courted by this

male permit copulation until they had been lifted in this fashion. This male became sexually active at 14 months; females can breed at 10 months.

At birth the young hide under thick grass or even within the exposed root system of trees and remain hidden for three or four days without moving except to suck. Thereafter they begin to follow the mother but still seek shelter from time to time. Growth is extremely rapid and near adult height is achieved in about three months.





Klipspringer (*Oreotragus oreotragus*)

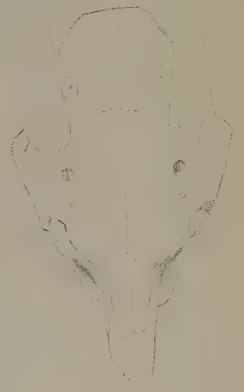
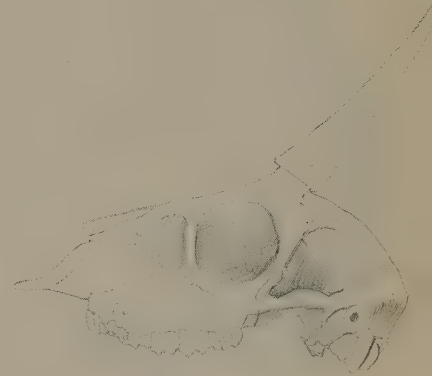
Races

<i>Oreotragus oreotragus saltatrixoides</i>	Type Ethiopia (Temmincki, 1853)
<i>Oreotragus oreotragus somalicus</i>	Type Northern Somalia (Neumann, 1902)
<i>Oreotragus oreotragus centralis</i>	Type Zambia (Hinton, 1921)
<i>Oreotragus oreotragus aceratos</i>	Type South-East Tanzania (Noack, 1899)
Races of dubious validity	
<i>Oreotragus oreotragus aureus</i>	Type Northern Kenya (Heller, 1913)
<i>Oreotragus oreotragus schillingsi</i>	Type Northern Tanzania (Neumann, 1902)

Klipspringers mostly inhabit tumbled labyrinths of rocks on steep, rocky and well-drained hillsides, escarpments or valleys or open screes of loose pebbles or cinders. They are sometimes far from water. At higher altitudes they are often exposed to extreme fluctuations of temperature. They are vulnerable to large raptors and to leopards.

They have a variety of adaptations to cope with these hazards. Their colouring is a rock-like freckle of yellows and greys and this camouflage is augmented by their ability to remain motionless for long periods and a capacity to avoid panicky flights. Unlike so many other antelopes they do not have a conspicuous wagging tail; instead they carry their freckled grey haunches low. Movements are fast and liquid only to be frozen again into immobility. A sudden flicker of the large white-lined ears may precede a standing leap that takes the body twisting through space up on to some unlikely foothold a metre or more above and then a series of jack-knifing bounds up the hill and out of sight. Their weight is taken straight down on to the flat, blunt tips of their hooves, which can find a purchase more readily than a conventional hoof, and their rubbery texture prevents them from slipping easily. Their sight is acute and, since they generally have a high vantage point they are likely to see most predators before they themselves are seen. The eyes are widely spaced, whereas the nasal area is narrow, with the result that this species has a peculiarly short, wedge-shaped face and a reasonable measure of binocular vision. Possibly this helps the animal to judge distances and planes while jumping over rocks.

The fur is extraordinarily brittle and coarse to the touch but very light in weight. The greyish-white hair resembles that of the prongbuck, *Antilocapra*, or the water deer, *Hydropotes*, is very loosely rooted and only the tips are pigmented. Each hair is hollow and contains air most of its length. Because the hairs are swollen by an airy core and because they grow rather densely they cannot be sleeked to hug the form and a klipspringer's body,







Klipspringer (*Oreotragus oreotragus*)



Family Order Local names

Mbuzi mawe, Ngurunguru (Kiswahili),
Atiri kiki (Karamojong, Turkana),
Engine-o-soito (Masai), Mvusia
(Kibungu), Engisin (Samburu),
Chepurrbetiandet (Sebei), Ogwa (Lugbara),
Atut, Lacekgweng (Lwo) Lakud (Somali).

Bovidae
Artiodactyla

Measurements head and body

85 (75—90) cm

height

49 (43—51) cm

tail

6.4—10.5 cm

weight

8—18 kg

Average weights vary
regionally between

10—15 kg

horns

8.5 (6—15.8) cm

therefore, appears much more chubby and heavily built than is really the case. Nonetheless, it can, like any other antelope, shimmy its fur with a well developed dermal muscle and its fur may stand on end if the animal is hot or sick. Fluffing out the fur may allow air to reach the skin and so cool the animal, and tightening the coat presumably traps a blanket of air which retains the body's heat. Considering the exposed conditions in which many klipspringers live and the temperature changes they may have to face on some mountains (from frost at night to 42°C. during the day), temperature regulation becomes a major problem, and it is likely that the hollow hairs are a simple thermoregulating device. Dorst and Dandelot (1970) suggested that the coat might cushion contusions or bumps, but this could only be an incidental benefit, since klipspringers are too surefooted and agile for such accidents to be common.

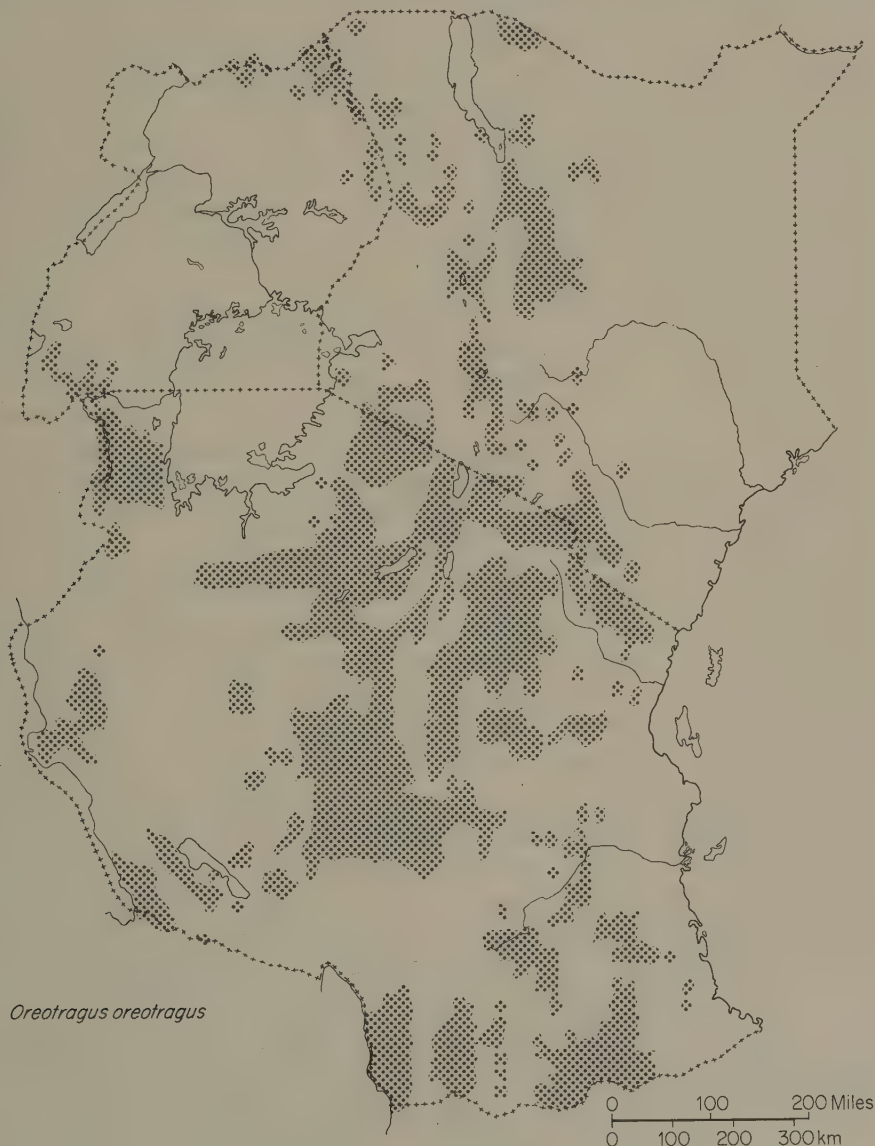
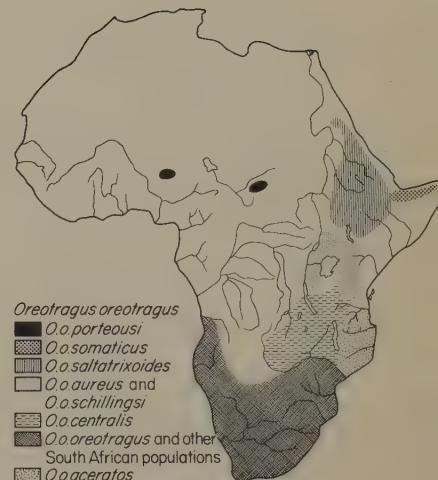
The males have short, upright horns and in some populations in Tanzania, Karamoja and Ethiopia a high incidence of females with horns has been reported, but this is not a consistent characteristic of any particular population.

Klipspringers occur from the Cape to Angola and throughout the drier, rougher areas of eastern Africa to Ethiopia and the Red Sea hills in Sudan. They are also reported from a few isolated massifs in Nigeria and the Central African Republic, which suggests that their distribution along the southern margins of the Sahara may have been more extensive in the past.

In a species with a discontinuous distribution racial differentiation is to be expected. Differences in coat colouring between regional populations have some correspondence with ecological and geographical entities, but in the absence of adequate information a review of the klipspringer's subspecies would be premature. It should be noted, however, that for the two races described from type specimens of East Africa provenance, *O. oreotragus aureus* (Heller, 1913) and *O. o. schillingsi* (Neumann, 1902) none of the supposedly diagnostic characteristics describe a recognizable population. East Africa, as is often the case, seems to have been the scene of a complex interaction, or mixing, of populations and the klipspringers in Uganda and upland Kenya show considerable variation, in which individual colouring might be influenced by unknown factors such as age, physiological condition, or the combination of different genetic patrimonies.

The most favourable and extensive regions for the klipspringer are southern and north-eastern Africa, where the vicissitudes of climatic change are unlikely to have affected the klipspringer's habitat as much as they might have done in tropical Africa. In East Africa the best klipspringer habitats follow the course of the Rift valleys but they are nothing like as extensive and homogenous as they are in Ethiopia, which is the most likely centre of evolution and is inhabited by a recognizable population, *O. o. saltatrixoides*. South of the Zambesi klipspringers can all be referred to *O. o. oreotragus*.

Klipspringer populations adapted to semi-arid conditions extend from northern Somalia as far south as central Tanzania. Animals from this area, of *O. o. somalicus* type, are a bleached creamy yellow graduating into grey on the legs with pale sepia hocks. By contrast, animals from moister habitats in South-eastern Africa, *O. o. aceratos*, have strong colour contrasts with golden yellow forequarters and back, a grizzled grey rump and muzzle and



black hocks. The Rufigi River is the northern boundary for this race but it intergrades with the Central African race, *O. o. centralis*, in southern Malawi. In South-eastern Tanzania some individuals of the *O. o. centralis* type, notably young animals, have a rich russet tinge to their shoulders or flanks with less or none of the typical pepper-and-salt grizzle. This is due to the hairs lacking the usual dark sub-terminal band, they are also soft and pliant in texture, particularly so just behind the elbow. While bold colour contrasts and patches of softer fur are most apparent in animals from the humid uplands, a tendency towards this type of colouring is apparent as far north as Uganda. It is unlikely that the association of less specialized fur with an area of conspicuous colour difference is without biological significance; perhaps the tendency to scent the coat with facial secretion while grooming gives certain areas a target value during interactions.

In East Africa klipspringers occur up to 4,000 m on Mt Kilimanjaro and they are common on the summit of Mt Meru (4,500 m) as well as on the ash cone within its crater, where the cinders are sharp and loose. They are abundant on similarly inhospitable lava flows throughout Kenya. They do not occur on the wetter mountains flanking the western Rift.

Varying densities of klipspringers in two gorges and an escarpment in Ethiopia offered Dunbar and Dunbar (1974) the opportunity to investigate the species' habitat preferences. Bush cover was not found to be a critical factor, whereas the amount of ground cover had a very positive correlation with the animals' abundance.

KLIPSPRINGER DENSITIES IN THREE ETHIOPIAN LOCALITIES
(from Dunbar and Dunbar, 1974)

Locality	Klipspringer density	Percentage ground cover	Percentage bush level cover
Simien escarpment	46.7 per sq km	77.4%	30.5%
Simien gorge	19.1 per sq km	52.0%	43.7%
Bole gorge	13.4 per sq km	36.8%	12.0%

The percentages were considered to reflect the animal's feeding preferences, which were also investigated by Dunbar (1978). Grass constituted 17.3% of their diet, herbs 52.9%, shrubs 7.5%, bushes 16.9%, creepers and lichens 3.8%.

Wilson and Child (1964) recorded only 10% grass in the diet of klipspringers in South-central Africa and this was mainly freshly sprouted grass growth; the leaves, buds, small twigs and bark, fruit, seeds and pods of a very wide variety of herbs, shrubs, trees and other plants constituted the rest of their diet. The fruits of *Acacia* spp., *Dichrostachys*, *Pseudolochnostylis maprouneifolia* and *Ficus* spp. have been recorded and *Commiphora*, *Grewia*, *Brachystegia*, *Euphorbia tirucalli* and *Vellozia equisetifolia* leaves have been noted as favourite foods in thicket and woodland habitats.

Their feeding is mostly highly selective, and leaves are plucked at ground level or within easy reach of their neck. Some well-drained hillsides tend to become very bare during the dry season and the klipspringers are deprived of food, cover and shade by drought and fire. In these circumstances they

may move down to the base of escarpments and may even take cover in clumps of vegetation in the vicinity of ground water and springs. It is during the dry season that klipspringers move furthest from the hills and I have found them out in the flats feeding on fresh burns in the early morning, half a kilometre from their rocky outcrop home (drying out of the soil probably allows them to extend their range as they are visibly incommoded by soft muddy ground). At such times klipspringers from several different hillsides may converge on a local flush of vegetation. During the dry season, I have seen nine adult animals together just after dawn at the lower and moister end of a long low ridge in the floor of the Kenya Rift Valley. They were viewed from a hot air balloon and, being disturbed, ran silently up along the ridge in a long line, separating out as they progressed, which suggested that they were returning to the normal social pattern of pairs or trios spaced out along the hillsides.

It is rare for a klipspringer to remain solitary for very long. A female is generally attended by a male and she may be accompanied by a young one or another female (perhaps an adult offspring). Of the groups recorded in Ethiopia by Dunbar (1978) 20% were of one male with two females. Similar ratios were recorded by Wilson and Child (1964) in South-central Africa. A breakdown of sexes from their records of shot animals revealed that males are the most frequently seen (52 males to 38 females) and there are also more males than females in most museum collections. This imbalance does not reflect a true sex ratio but rather the tendency for males to take up more prominent positions in their territories. As in the instance just described, when aggregations of seven or eight animals are seen, these are probably temporary feeding assemblages that take place outside the normal home range when food is scarce there and when territorial behaviour is in abeyance.

In Serengeti, Walther (in Grzimek, 1972) noted that klipspringers disappeared from their usual haunts among the rocks for the duration of the dry season. At the beginning of the rains he saw an assembly of six animals which, in the course of the next few days, re-tenanted the boulders in pairs. If such parties remain together during the entire period of drought it would be interesting to learn more about the accommodation they make to one another.

In Ethiopia, Dunbar (1978) recorded klipspringers spending 30% of the day in cover and 35% actively feeding. There were three alternating periods of activity and rest; feeding occurred in between with a distinct peak in the later afternoon.

When grooming themselves, an activity that commonly follows the long afternoon rest, facial secretion rubs off on to shoulders, flanks and legs. The cheeks and ears are frequently scratched with the hindlegs and pairs often lick one another's face and glandular area. When the fur is groomed, the animal licks deep into the coat (apparently down to the skin) and then shimmies the fur back into place by spasms of the dermal muscle.

The fur of the anal region is not differentiated in colour and the raising of the short tail for excretion is performed in an unobtrusive crouch. Excretion may precede a bout of activity but a dung pile is normally used, to which the animal must walk.



During the heat of the day, klipspringers generally rest up on their own but with another animal nearby. I have noted an adult male standing quite still in the same place, and intermittently chewing, from 10 a.m. to 3.50 p.m. A free-ranging captive ruminated at night after its evening feed and it also fed on moonlit nights. Nocturnal activity in wild klipspringers is widespread but has not been quantified.

When an animal is disturbed it may either freeze and keep quite still or it may flee. Walther (in Grzimek, 1972) has reported a curious manifestation of the "freezing" habit in three captives which were to be caught and transferred from a small pen. "When the keepers were about to grab one, it escaped, ran to one of its fellows, held its head under the other animal's body and then it could be seized without further trouble. The next one did the same and the last one, for lack of anything better, stuck its head into a corner of the stall." Perhaps these captives were recapitulating an infantile creep-for-shelter tactic, or else they may have been employing a juvenile tactic for escaping male aggression, sheltering beneath a female.

When the field is free for a flight, which is generally uphill, the animal is quite likely to turn round after the initial run. Out of 20 flights observed in Ethiopia, it was usually the male that stopped and turned to inspect: only once did a female turn (Dunbar and Dunbar, 1974). These authors recorded a similar prominence for the males during ten minute activity counts; the males were seen feeding 21 times to 98 times standing, while the females were feeding 47 times to 78 times standing. Both sexes utter

loud whistles during or after a flight but there may also be a male predilection for this habit. The calls are sometimes repeated at five seconds intervals in series; they have strong directional properties, allowing the caller to be located over considerable distances. Norton (1979) suggested that whistles uttered from a prominence might demonstrate a klipspringer's fitness to a predator and the uselessness of pursuit. Dunbar and Dunbar (1974) prefer the traditional interpretation of the male's role as a look-out and warner against predators. Whistles might have acquired both these functions but they are probably subsidiary and have certainly derived from their primary role as an acoustic advertisement from one territorial animal to its neighbours.

The idea of an alarming function for whistles is somewhat vitiated by the observation of companions continuing to rest and feed while one animal is whistling. On the other hand, members of a group may respond immediately to less obvious signals, if the ears are flashed back and forth, the feet stamped or if the animal makes a breathy snort just before it runs. These signals too may have a communicative function as well as alerting other klipspringers to danger. A klipspringer seldom runs very far if it is disturbed within its home area and this might be determined by a reluctance to invade neighbouring territories, from which any intruder is immediately chased.

Klipspringers make dung deposits, choosing areas of flat, sandy soil, not rocks; Dunbar and Dunbar (1974) rarely saw these in the heart of their territories, (which were estimated to be 6–8 ha in extent) but rather near their boundaries. Unlike other small antelopes they do not paw their dung-piles and they lack pedal glands. Preorbital glands are prominent in both sexes and most of the twigs, grass stems and some of the rocks throughout the more intensively used areas of a home range have deposits of the facial secretions if they are at face level, and a free-ranging tame male repeatedly bit off grass tops and then inserted the stalk into its pre-orbital gland.

In Ethiopia Dunbar and Dunbar (1974) observed that marking with the preorbital glands mostly coincided with a conspicuous increase in the size of the glands in September, the only month in which sexual interactions were seen. They saw a male and a female mark alternatively on the same spot and postulated that scent-marking in klipspringers might relate to sexual behaviour and the creation of pair bonds. They found some evidence for a mating season in Simien during September, which would result in births during the early rains in April–May. In Sankabor fawns were first seen at the end of the rains in November, which would imply matings in January or February. Wilson and Child (1964) recorded that a minimum of 67% of all sexually mature females collected in eastern Zambia were either pregnant or lactating. In this area births were scattered throughout the year, but elsewhere there may be birth peaks. For example, Cuneo (1965) recorded that captive females in Naples only came into oestrus between July and December. The long gestation period of about seven months probably encourages irregular timing of births, but it would be interesting to know whether dry seasons affect the frequency of births in East Africa, particularly if territorial behaviour tends to be in abeyance at this time.



Cuneo (1965) noted that a captive male only attempted to court a female while she was in oestrus but remained tolerant of other females in the group. The female was seen to be mounted five or six times in the course of about a week. The male has been heard to make a humming noise while copulating.

After the kid is born it hides and is only visited by the mother briefly for suckling, which takes place three or four times a day. The young have a bleating contact or want call. At about one month the kid starts to accompany the mother but it may return to its hiding place to rest until, at the age of three months, it follows the parent in all activities. Hauser (1943) noted that a captive female followed him very closely wherever he went, having probably become imprinted on him. Another female, reared with goats in Acholi, could be herded with them, but a male that was hand-reared on Kikagati Island in the Kagera River, became more independent. Dunbar's observations in Ethiopia suggest that the pattern of development differs between the sexes. Young males were seen associating with the parental or neighbouring groups, after which they were thought to pass through a stage of lacking a precise home range before acquiring a territory.

Young females frequently remained with the parents and the second female might breed within this enlarged unit. Movements were more frequently initiated by females than by males.

Young klipspringers are somewhat reminiscent of goat kids and sometimes bounce up-and-down with fore-and-aft rocking jumps without leaving the prominence they are standing on. Unlike goats they fight with chest low and legs thrown forward and splayed, each contestant trying to stab his opponent from below while parrying the counter thrusts. Captive males have been seen to bite at one another. Growth is rapid and at one year the animal is sexually mature.

Sex ratios favouring females may reflect the disadvantages of young males going through a stage of lacking a permanent and well-known home range. There is evidence that the animals have favourite retreats where their colouring helps them to escape detection. Within a well-known territory the security of certain hiding places may be tested by experience. At Chapota in Ufipa, a farmer's dogs were in the habit of pursuing the local klipspringers. They were regularly seen to run up a tree leaning about 60° from horizontal and run out on a relatively slender branch (Dam, personal communication). Perhaps trees offered the best refuge to the Chapota klipspringers in response to those particular predators, but jackals and wild dogs are probably less dangerous to klipspringers than leopards, caracals, serval cats, eagles and pythons, all of which have been reported to prey on this species. A most dangerous hazard for the new-born is probably baboons. Even adults may not be immune; for a female has been seen to be killed and eaten by a troop. Baboons share the klipspringers' habitat throughout their range but the two species normally do not pay much attention to each other.

Hyraxes, dik-dik and Sharpe's grysbok are possible competitors for food during the dry season.

Klipspringers suffer from ticks and hippoboscids. Sometimes the removal of such external parasites seems to be undertaken by redwing starlings, *Onycognathus morio*, (Lee, 1963; Angwin, 1971); for these mountain-dwelling birds have been seen hopping on the back and neck of klipspringers and pecking about in the fur. One doe was seen to put her head down to allow a bird to continue its search in her ears.

Klipspringers sometimes continue to survive in rocky outcrops long after cultivation and hunting have removed other ungulates from the surrounding country, but they are susceptible to both snaring and shooting: the former because of their regular habits and use of dung middens, the latter because they tend to expose themselves on vantage points.

Populations in Zululand and Rhodesia have been reported to survive fairly intensive shooting during tse-tse clearing schemes, but competition from goats and sheep and dense human settlement with very persistent hunting and habitat change is likely to exterminate them altogether.



Dik-dik
(Madoqua)

Family

Bovidae

Order

Artiodactyla

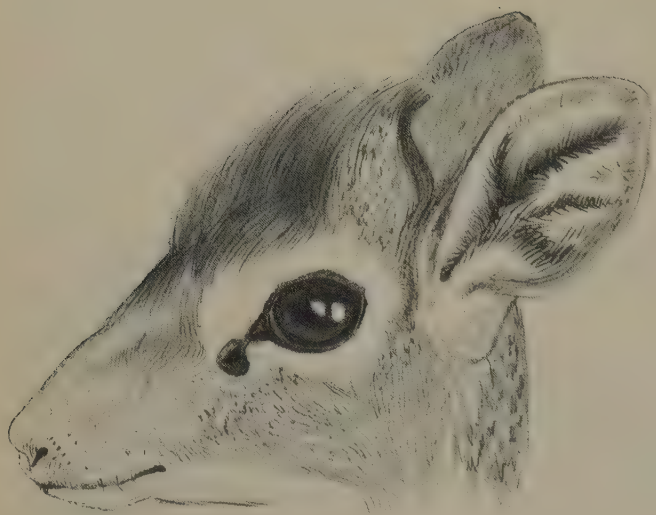
Local names

Digidigi, Suguya (Kiswahili), Kabii (Kikamba), Nguyhuya (Kinyaturu, Kisandawe), Shigaro (Dorobo), Esoro, Ethuro (Turkana), Esiro (Karamojong), Seran (Sebei), Wisi (Kiliangulu), Tibi (Kipokomo), Empanas, Eng-omani (Masai), Kizimba (Kisagara), Chizimba (Kigogo), Sala (Kisukuma), Erongo (Samburu), Gussulei, Sakaro (Somali).



Above: *Madoqua guentheri*, male.

Opposite: *Madoqua guentheri*, female



Madoqua saltiana.



Madoqua kirkii.



Madoqua guentheri.

Dik-dik (Madoqua)

Measurements head and body

52—67 cm

height

34.5—40.5 cm

tail

3.5—4.5 cm

hindfoot

17—20 cm

weight

2.7—4 kg

horns

5 (3.6—8.8) cm

Madoqua saltiana swaynei

head and body

60—72 cm

62.5 cm female average

59.0 cm male average

height

35—43 cm

tail

4.5—5.6 cm

hindfoot

16—19 cm

weight

5.5 (4.5—7.2) kg females

5.1 (3.8—6) kg males

horns

7.5 (6.0—11.4) cm

Madoqua kirkii

head and body

64 cm female average

60 cm male average

height

34—38 cm

tail

3.5—5 cm

hindfoot

19.5—21 cm

weight

3.7—5.5 kg

horns

7.5 (5—10.8) cm

Madoqua guentheri

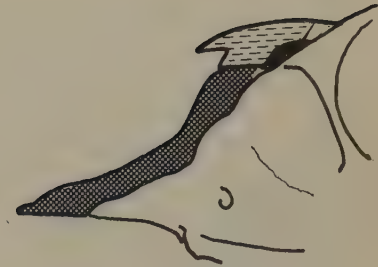
Species and races

Madoqua saltiana swaynei, *Madoqua kirkii kirkii*, *Madoqua guentheri*

Madoqua saltiana Endemic to Horn of Africa, arid-adapted, predominantly nocturnal species. Least specialized nose, well-developed nasals and premaxilla.

Madoqua kirkii Eastern and South-West African semi-arid adapted, diurnal/nocturnal species. Moderately specialized nose. Reduced nasals and premaxilla.

Madoqua guentheri North-East African endemic, arid-adapted, predominantly diurnal species. Highly specialized nose, very reduced nasals and premaxilla.



Dik-dik (*Madoqua*)

The three species of dik-dik (there is a fourth on the Somali coast) represent a distinctive gradient in the adaptation of a very small antelope to heat and desiccation. The most obvious external manifestation of this adaptation is the modification of the nose into a flexible bellows-like mechanism for cooling the blood.

Paradoxically, the less specialized *Madoqua saltiana* occupies the most arid areas but this species probably avoids excessive overheating by lying up in shade during the day and restricting most of its activity to the night (Simonetta, 1966). It inhabits thickets in which the dominant woody plants are *Acokanthera schimperi*, *Buxus hildebrandtii*, *Acacia* and *Commiphora* spp. This type of evergreen scrub, which is characteristic of the eastern foothills and outliers of the Ethiopian mountains, supplies the dik-dik with a year long food supply and good cover to shelter in.

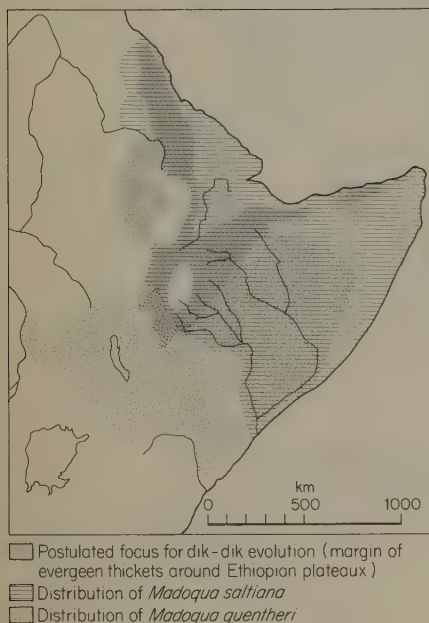
M. saltiana is distributed all along the fringes of the Ethiopian massif and follows down the valleys that drain to the east and it occurs wherever there are evergreen thickets along the coasts of Somalia and Eritrea (Yalden, 1978). One of the tributaries of the Juba River brings this species into East Africa in the vicinity of Mandera.

Madoqua kirkii and *Madoqua guentheri* are often distinguished as a separate genus or subgenus, *Rhynchotragus*, on account of the longer proboscis. Since the characteristics held to separate these two artificial groups are graduated, such splitting only serves to obscure the essential homogeneity of the dik-diks and, in my view, should be abandoned.

M. kirkii is a widespread and successful species in the drier subtropics of South-western Africa and in eastern Africa. There are local differences in the tonality of coat colour which correspond with relative humidity and regional differences in size (which may reflect diet) but, until such traits can be defined, it is probably more useful to regard the eastern African population as one race and the South-West African *M. k. damarensis* as another. Judging by the small degree of differentiation, the two populations must have been through the connecting "drought corridor" during relatively recent times (see Vol. I, pp. 60—63).

A greater age for the more conservative *M. saltiana* is implied by its having differentiated into ten forms, which were formerly grouped under five species (Allen, 1939). However, the nomenclature of this group has been revised and simplified by Yalden (1978). It is clear that the Horn of Africa with its very peculiar climatic and ecological conditions has been the focus for dik-dik evolution and that *M. kirkii* has been the only species to expand far southwards.

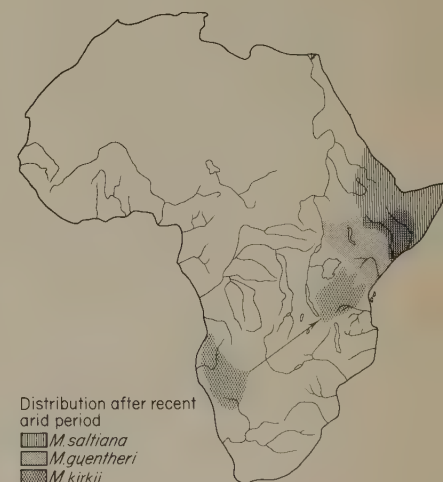
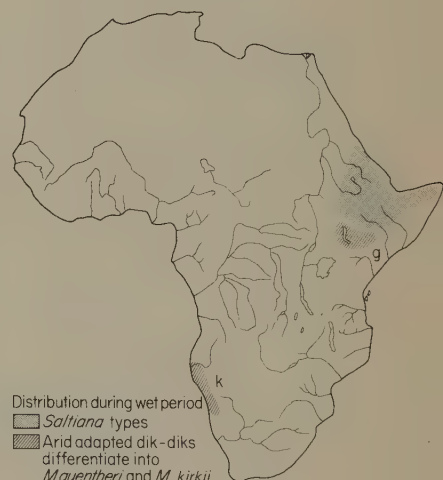
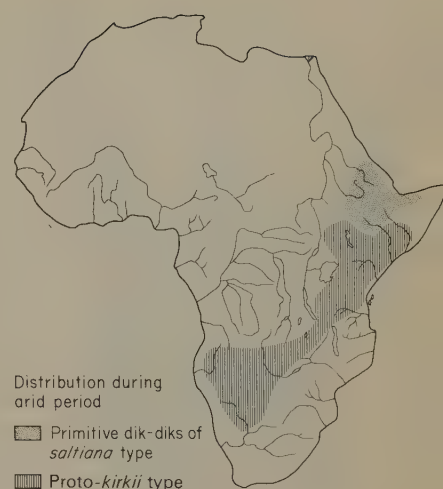
M. kirkii must have derived from a parental stock having much in common with the conservative *M. saltiana*. The restriction of the latter to the Horn may have much to do with the animal's dependence on dense evergreen growth. To the north and west droughts have probably been a perennial factor inhibiting expansion. Towards the south, scarcer food and shelter in the arid Lake Turkana (Rudolf) basin may not have been at critical



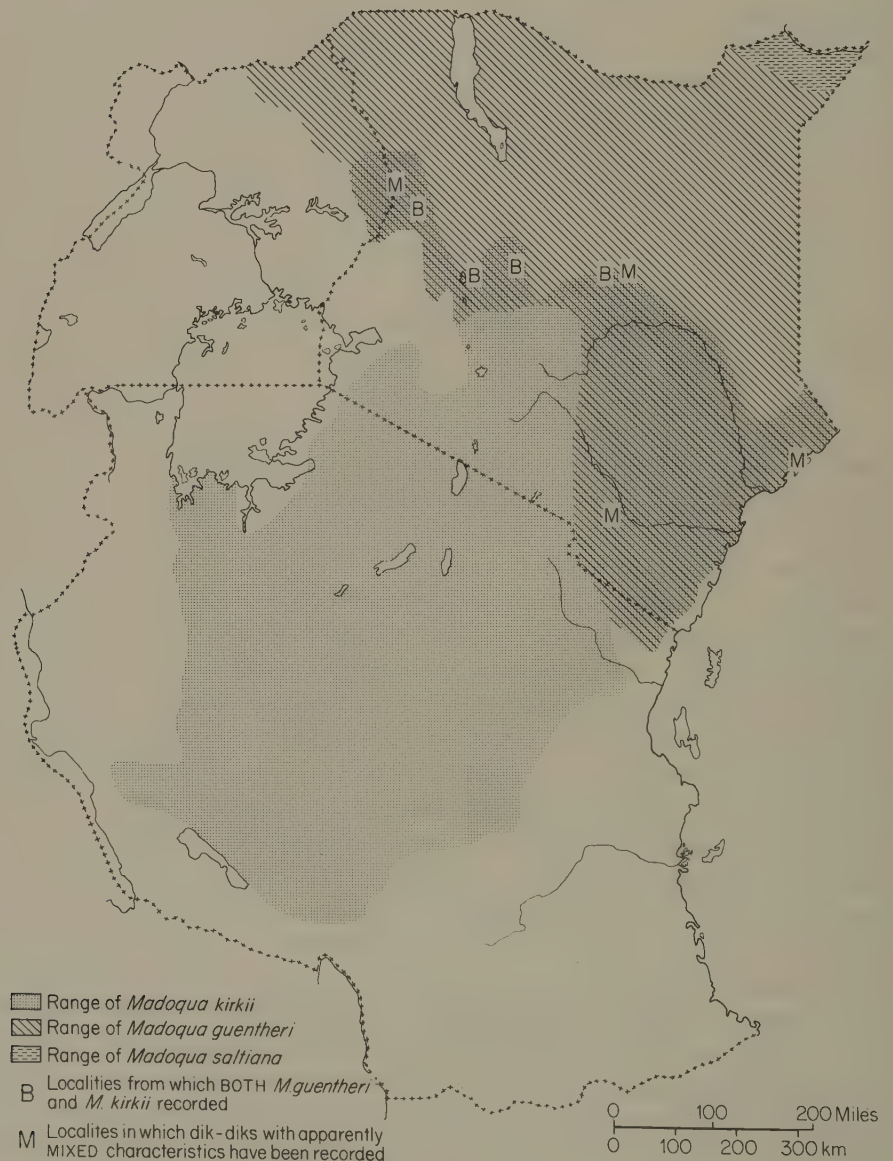
levels during dry periods, but the ancestral dik-dik of this region might have been pushed into hotter, more exposed habitats and longer activity periods. Further development of the nasal cooling chamber would accord with such environmental pressure and the absence of a significant overlap in the ranges of *M. saltiana* and *M. kirkii* is not inconsistent with the latter being regarded as an only slightly more advanced derivative that has broken out of its regional cul-de-sac.

Regardless of whether it was ecologically superior or not, drier phases of past climatic fluctuations would have opened up very extensive areas of suitable habitat in equatorial East Africa and beyond to dik-diks from the southernmost part of the Abyssinian region. Like other equatorial populations, dik-diks would then have been separated and brought together by climatic changes and the relationship between *M. kirkii* and *M. guentheri* can be tentatively explained by invoking past climates. There are two possibilities: the first and the most likely depends upon there having been at least two dry periods when South-western Africa was ecologically linked with eastern Africa. The first connexion established *M. kirkii* on the western side of the continent. During subsequent isolation the East African population, still centred around the hot Turkana basin, and continuing the trend towards a more and more efficient nasal cooler, gave rise to the long-snouted *M. guentheri*. The second period of re-connexion with southern Africa is needed to reintroduce the less specialized but ecologically more versatile *M. kirkii* into all but the hottest environments or those pre-occupied by the long-established *M. saltiana*. In the process it may have competed with and extensively replaced its sibling species *M. guentheri*. The second and less likely possibility is that *M. kirkii* and *M. guentheri* differentiated within East Africa, a forest belt having temporarily separated their common parental stock. In which case, the south-western dik-diks are merely a recently isolated offshoot of the East African *M. kirkii*. The contemporary distribution pattern suggests that *M. kirkii* is ecologically the most versatile species but is excluded from most of the Horn by the presence of other dik-dik species.

While there is insignificant overlap with *M. saltiana*, the interaction with *M. guentheri* is more complex and interesting. There is a narrow belt over 1,000 km long where the margins of the Lake Turkana basin and the Somali interior meet the moister habitats fringing the Kenya highlands and the coastal strip. North of the Tana River, *M. kirkii* does not extend beyond the isohyet for 50 cm mean annual rainfall or the boundary between savanna and dry bushland (as shown in Vol. I, pp. 13 and 24). Along this interface the two species meet and in places exist side by side without any interbreeding (Hollister, 1924; Hofmann, 1973). However, skins and skulls from localities as far apart as the Webbe Shibeli River (Somalia), South Turkana and the Kenya-Uganda border display intermediate or mixed characteristics (Coe, personal communication; Ansell, 1968) suggesting that hybridization although rare is widespread. Furthermore, strongly reduced premaxillae in some *M. kirkii* specimens (notably from Tsavo and Manda Island) (p. 248), could imply that past mixing between the two species may have left its mark in dik-diks which are now some distance from the zone of interaction. This would support the idea that *M. kirkii* is an ascendant species



in all but the driest habitats and that it is genetically very close to *M. guentheri*. To explore the reproductive and behavioural mechanisms that, however imperfectly, keep the species apart, and to examine how the two species share out the habitat is an important area for future research. Would an increase in aridity see a shift in the *guentheri/kirkii* boundary in favour of the former? Does the latter expand with consistently higher rainfall? Are there differences in their activity cycles, densities and their food and shelter preferences? Detailed observations in Laikipia, Samburu and southern Somalia, particularly over a period of climatic instability such as the present, might help answer some of these questions. Likewise a study of *M. guentheri* and *M. saltiana* in their most extensive areas of sympatry might help define more precisely the part played by differing activity periods and the partitioning of food.



For the present it is only possible to present a compound portrait of *Madoqua* but it should be remembered that the primary effect of this modest radiation of species has been to increase their overall ecological range and diversify the responses of a very small ruminant to exceptionally difficult conditions.

In most arid habitats it is only possible for a very small ruminant to live within a limited area all the year round because there is little food in the dry season. Against this advantage of small size must be set the handicap of having to do without water yet needing to keep cool. This is problematic because the large surface area of a small animal relative to its weight heats up fast.

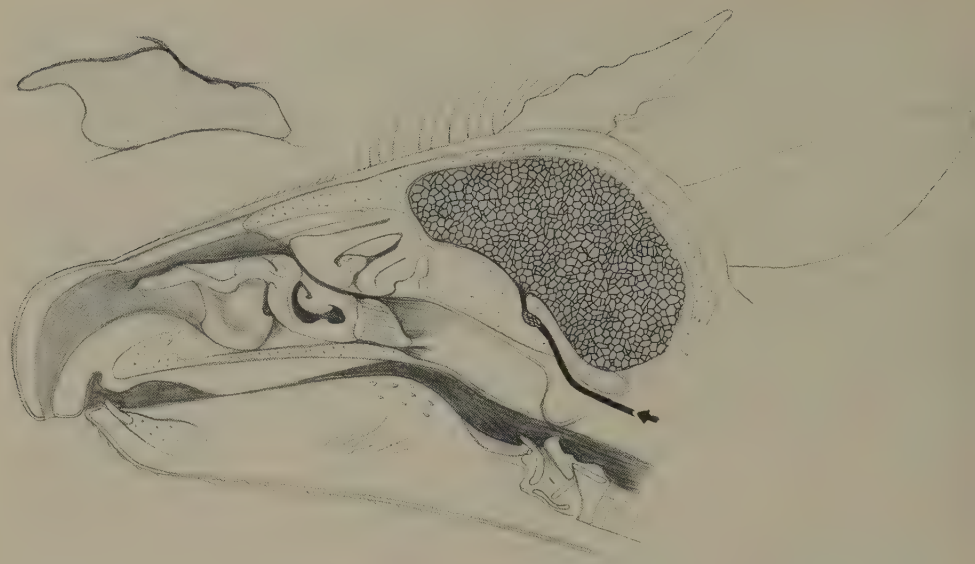
Dik-diks minimize heat production and reduce water loss by means of inconspicuous adaptations in the water economy of their kidneys and digestive tracts and in subtle adjustments of their activity cycles, but the specialized nose is probably their major cooling device. It is also the most obvious feature distinguishing them from other small ruminants living in cooler or less exposed habitats.

In a detailed study of the environmental physiology of the Karamoja dik-dik, Shoen (1972) discovered that they withstand intense heat loads by increasing their respiratory rate. After eight hours at 40°C the normal 50–60 cycles per minute rise to nearly 400 cycles per minute. In experiments conducted in a climatic room Hoppe (1977c) found that the body temperature of a running dik-dik rises from a resting value of 38.5°C to about 40°C within two minutes, after which he measured respiratory rates in the panting animal rising to as much as 500 cycles per minute. To find out how much energy is expended during the normally vigorous activity of panting, Hoppe and his colleagues measured oxygen consumption and much to their surprise found that energy consumption in a panting dik-dik is as much as 42% lower than when an animal is quiescent. The explanation probably lies in a 50% decrease in blood flow to all but the muscles involved in respiration (Hoppe *et al.*, 1975). Arterial blood is probably diverted from other parts of the body to the moist membranes of the oral and nasal cavities where the rapid panting passes a continuous stream of dry air over the nasal mucosa, evaporation cooling the moist black lining of the proboscis together with its underlying blood vessels. Studying domestic sheep, Baker and Hayward (1968) found that blood from the nasal linings drained back to the cavernous sinus just below the brain. Here cooled blood surrounds a *rete mirabile* of the carotid artery carrying blood to the brain, and these authors demonstrated that an exchange of heat takes place here. The dik-dik seems to have carried the adaptation still further, enlarging the vestibule of the nose and turning it over to serve as a cooler for the blood. Acting like a bellows, its muscular flexibility can enhance control over airflow and therefore improve the efficiency of its evaporative surfaces. *Saiga tartarica*, an Asian antelope with similar but still larger nose, is said to use it to filter dust and to achieve thermostatic control over the temperature of inhaled air, but cooling blood temperatures should be even more important for an animal living on exposed plains under an extremely fluctuating climate.

The advantages of evaporation taking place within the nasal chamber are that it is selective in its effect and economical in overall water loss. The most



Madoqua kirkii, female.



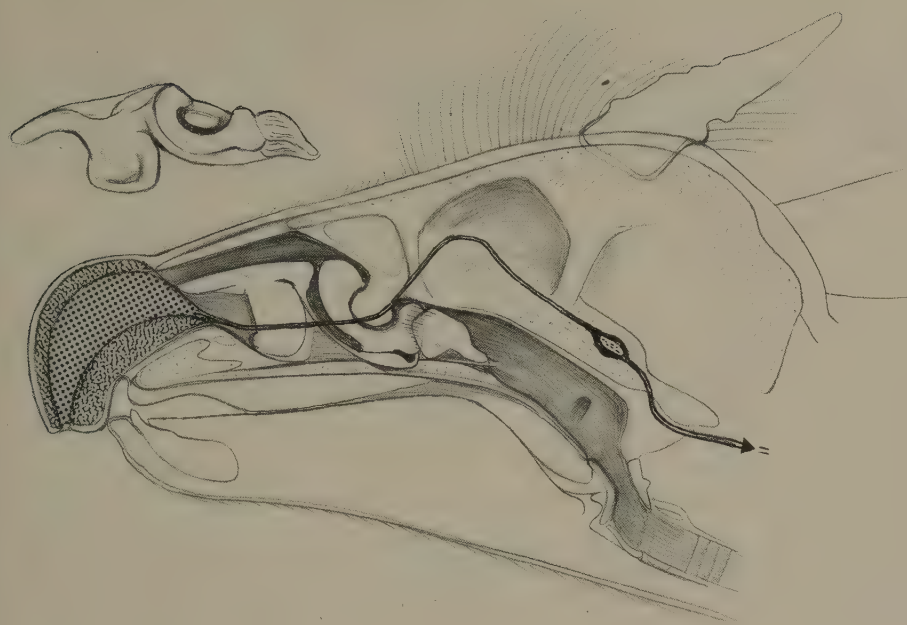
Cross-section of dik-dik head. The arterial blood supplying the brain is indicated and a *rete mirabile* in the cavernous sinus is suggested. The maxilloturbinal "whistle" is shown isolated above and *in situ* below. The inner surface of the right turbinal is displayed and the oesophagus is illustrated with the epiglottis closed.

immediate danger of overheating is its effect upon the brain and the fact that it is blood *en route* to the brain that is cooled first and most thoroughly is a parsimonious but very effective adaptation. Although dik-dik start panting as soon as their temperature rises, Shoen (1972) found that overall body temperature fluctuations covered a span of nearly 6°C above the normal.

Since all the dik-diks' water needs have to be extracted from the plants they eat, they use what they have with exceptional economy. Comparing the dik-dik with antelopes from moister habitats, Shoen (1972) found that dik-dik deprived of water are able to reduce their faecal water loss by about half. They also employ their specially adapted kidneys to so concentrate urine that a mere 30% of the total water loss is voided by this route, compared with 65% in an eland. Of the water lost by evaporation only a tiny proportion is sweated because the sweat glands, although present, discharge about one-twentieth of the moisture exuded by a human (Hoppe, 1977c). Minimal performance of the sweat glands reduces water loss over a relatively large body surface, but overheated animals sometimes compensate for slow body cooling by spreading saliva over their flanks.

Water droplets exuding from the nose and immediately swallowed by the dik-dik were seen by Hoppe (1977c) as an indication that the proboscis might help reduce the amount of water vapour lost in expired air. Considering the dik-dik's elaborate water-saving system, the appearance of droplets in the nose suggests that this is the site for its major water losses. Such copious production of so precious a commodity only serves to emphasize the importance of the proboscis' function as an evaporative cooler.

The cross-sections above illustrates how this cooling mechanism may work and also shows the extent of associated morphological changes and a remarkable modification of the ethmoid turbinal, which seems to have turned over to function as a whistle.



Cross-section of a dik-dik's head. Shows vestibule of nose served by blood vessels in the mucous membranes. Venous blood shown going to pool in the cavernous sinus. The outer surface of the modified maxilloturbinal is shown from the left, with an overlapping process of the ethmoid turbinal. The whistle-like organization of this structure is shown above. Note the simple structure of the glottal region, which is shown in breathing position.

The colouring is interesting in that, although it is subdued and subservient to the overall cryptic effect, the legs and crest are plainer and warmer in colour, while the neck and rump tend to have a cool grey grizzle. The eye margins, ears, belly and buttocks have white or very pale fur and the last-mentioned is a particularly important signal device. This colour scheme is common to all dik-diks but finds its most exaggerated contrasts in a Somali race, *Madoqua saltiana phillipsi*. Possibly more nocturnal habits require greater visual emphasis while a reduced level of predation by raptors might have allowed crypsis to be diminished. The implications of this colouring for the dik-dik's behaviour are discussed later.

The dik-dik is never seen far from cover and all its habitats are characterized by an abundance of low thicket vegetation. Nonetheless, it does not flourish in dense growth, where its movements and vision are obstructed and it is commonest in *Commiphora*, *Acacia* and *Colophospermum* communities which are disturbed or overgrazed; for instance, regenerating bush on abandoned fields is especially favoured. It also occupies hard pans and other alluvial areas. The frequency with which this species is seen along roadsides in dry bush country is probably influenced by the slashing back of the vegetation, so that the road verges produce an abundance of food at the right level.

On the edge of the Kalahari, kudu and zebra are very numerous and Tinley (1969) thought they might together encourage concentrations of dik-dik, the kudu keeping the shrub layer within one metre of the ground and the zebra keeping down the grass. Another important mechanism bringing food within reach of the dik-dik is the wasteful feeding of other browsers, of primates, rodents and birds which litter the ground with pods, buds, leaves and flowers for the dik-dik to pick up. Lamprey (1963b) estimated that the leaves of trees and shrubs make up about 80% of their diet in Tarangire, grasses 16.67% and the remainder consists of herbs and

sedges. The high proportion of grass might be a seasonal bias, and Tinley (1969) noted grazing only in the wet season. However, it was once not unusual for dik-dik to come into gardens in Singida, Dodoma, Moroto and other small towns to feed on lawns and flowerbeds and they evidently have a varied diet. In Shinyanga, Harrison (1936) noted that dik-dik commonly eat sand and he also listed the following seasonal changes in diet:

Dry season	Wet season
<i>Acacia pennata</i>	<i>Acacia senegal</i>
<i>Combretum</i> spp.	<i>Commiphora schimperi</i>
<i>Fagara merkeri</i>	<i>Ipomoea</i>
<i>Grewia</i> spp.	<i>Leonotis nepetifolia</i>
<i>Harrisonia abyssinica</i>	
<i>Tamarindus indica</i>	

Hendrichs and Hendrichs (1971b) list Mimosaceae, Papilionaceae, Caparidaceae, Malvaceae and Anacardiaceae as supplying most of the dik-dik's food in Serengeti. Within these authors' study area, *Solanum*, *Indigofera*, *Hibiscus* species and *Microglossa oblongifolia* were the main food plants. They also watched a male sneak into another male's territory in order to feed on fallen figs.

In thickets most of the dominant plant species provide food for dik-diks and, in addition to those listed above, *Dichrostachys cinerea*, *Boscia*, *Capparis*, *Maytenus*, *Ziziphus*, *Salvadora* and *Terminalia* spp. have been recorded. Of cultivated crops they favour the growing buds of sesame. Simonetta noted that captives frequently changed their diet, favouring one food for some days and then refusing it for ten days or so, and Hendrichs and Hendrichs (1971b) note that protein content can fluctuate enormously in plants; they investigated the protein content of seasonal foods noting that some dry-season foods were particularly nutritious.

Food is selected carefully by dik-dik and then plucked with the tongue and upper lip. Browse that is inaccessible in a standing position may be reached by standing on the hindlegs and the roots of succulents may be exposed with the horns and gnawed.

Stomach contents from shot animals have weighed between about 300 and 500 g. Simonetta (1966) found that regular access to mineral salts helped maintain a captive breeding group in excellent condition and he thought that salt loss was responsible for several deaths, in which convulsions, subcutaneous oedema and paralysis were the most obvious symptoms. Captives drink when fed on dry foods but wild dik-dik probably go without drinking for most of the year.

The principal feeding periods are from dawn until mid-morning and from mid-afternoon until after dark. Differences in activity between populations have been discussed earlier and on present evidence, *M. kirkii kirkii* types seem to be more nocturnal than *M. guentheri* and the former sometimes continue feeding until about midnight, after which they rest until dawn. There is another short rest period spanning the midday heat. They usually sleep lying very close to a tree trunk, termitary or clump of thicket, some-

times with the head flat on the ground and the eyes closed, at which time they are extremely difficult to see.

Rumination occurs at frequent intervals during feeding and resting and nearly as much time is spent ruminating as feeding but for very short periods of only a few minutes.

Sometimes they are particularly active, such as during a full moon and Hendrichs and Hendrichs (1971b) established that *M. k. kirkii* on Serengeti moved over a larger stretch of country at night than they did during the day.

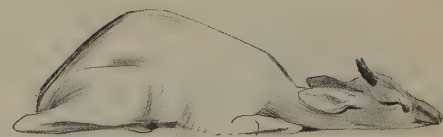
They tolerate quite cold night temperatures but a possible record for 4,300 m on Kilimanjaro (Swynnerton and Hayman, 1951) is almost certainly a misidentified klipspringer. A pet dik-dik kept in Switzerland went out into snow but tried to avoid wind and rain (Ziegler Simon, 1957).

Although male dik-dik sometimes stand about in the open and even lie down while exposed, they generally seek cover at the least alarm. I once had the opportunity to have a bird's eye view of a frightened dik-dik when gliding noiselessly over one in a balloon; the animal raced to the nearest bit of vegetation and crouched flat as we came directly overhead. I have also seen young ones sink down and flatten themselves. This strategy is commonly employed by adults against people, hyaenas and lions and they will even respond in this way to the warning cries of other animals. That they discriminate between predators is clear in their very different responses to hyaenas and leopards: the latter being watched from a safe distance and continually being whistled at. Hendrichs and Hendrichs remarked that a leopard moving off after some hours of this whistle-watching seemed to leave the male dik-dik quite exhausted with the tension. If, by contrast, a hyaena approaches a male close enough for it to have to break cover there is no whistling. Other known predators are cheetahs, caracals, serval cats, jackals, baboons, eagles and pythons. Simonetta (1966) saw a dik-dik that had been seized by a caracal put it to flight by kicking, although the dik-dik later died of shock.

They are well served by their excellent eyesight, alertness and speed. Simonetta timed a rush at 42 km per hour. However, their best insurance is probably knowing the home territory, which is shared by a pair, very well.

Even on casual acquaintance the different roles of the two sexes are perceptible in the watchfulness and restricted movements of the male and the greater mobility and more relaxed behaviour of the female. When chased, the animals also reveal their territorial inhibitions by following a circuit or constantly breaking back if forced. The role of predators in determining the size of a pair's territory is given some importance by Hendrichs and Hendrichs (1971b) and they state that a dik-dik's territory must be sufficiently large to leave the animal undisturbed refuge areas.

Estimates of the size of a territory vary widely and there is no doubt that this is partly due to real differences in density. It may also reflect the preoccupation of observers on central zones of maximal activity, or "cores", without account being taken of peripheral areas. Thus Tinley's (1969) estimate of a pair occupying 0.3 ha seems too small even in the best dik-dik country. The Serengeti dik-dik, living in isolated patches of thicket around rocky outcrops, were estimated to have territories of 5 to 30 ha. One outcrop



of about 50 ha supporting five pairs gave a fair average for this habitat. Hendrichs and Hendrichs have mapped these territories and charted the movements of males within them. Natural features such as drainage lines and paths often demarcate territories, even in apparently uniform bush. Simonetta thought that a regular network of grouped bush clumps with open ground in between—which he observed from the air—might correspond with natural territories. He saw pairs of *M. kirkii* spaced about 500 m apart in Somalia. My own estimates of spacing in over-grazed bush in Singida, Central Tanzania, and Nabilatuk, Karamoja, where dik-dik are most numerous, are of a similar order. Owen (1971) noted territories of 1.2 ha in Rumuruti.

Very occasionally groups of 8–10 animals may be encountered within sight of one another and Tinley (1969) suggests that related families with abutting or overlapping ranges may come together and that there might be seasonal patterns in the defence of territory. Hendrichs and Hendrichs, however, have established that large groups are generally attracted to a food-source in no-man's-land and that a life-long territory is formed which is occupied by a permanent pair and is always defended by the male against intruding dik-dik of either sex.

There are generally three animals in a territory and the female's first oestrus after the birth of a new young provides the mechanism for ejecting the subadult (Kellas, 1955). The oestrus, which lasts two days, elicits very aggressive behaviour in the male. In captivity, the subadult is sometimes tolerated again, but it is very rare to see four animals in the wild (Simonetta, 1966). Walther (1968) recorded an adult male charge its five months old offspring 50 times in one night. The fawn appeased these attacks by lying flat but few young animals can withstand such relentless persecution. The movements of a pair within the territory are not always co-ordinated, but they keep much closer together whenever they move outside their territory.

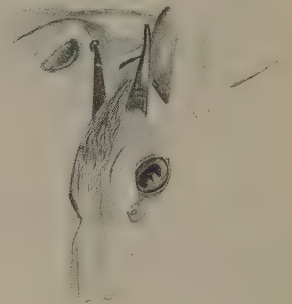
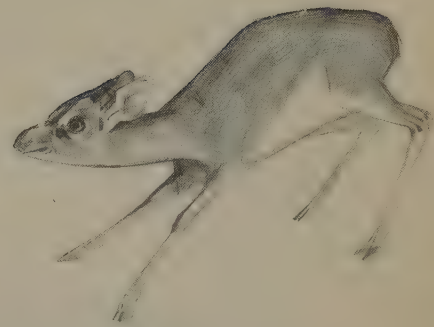
It has often been said that a shot dik-dik has its territory filled by a replacement almost immediately, but Drake Brockman (1910) noted that a female he shot had still not been replaced after seven months, likewise, it is common to see males apparently alone in their territories. Hendrichs (1975a) has followed the fortunes of a small group of dik-dik in Serengeti during periods four years apart and found that a pair is likely to remain together for life unless one partner is killed, but their territorial boundaries may change.

Simonetta (1966) has been able to follow the sequence by which two territorial groups of *Madoqua s. phillipsi* developed from a captive pair. The adult male offspring of this pair was initially persecuted by the father at the time of the mother's periods of oestrus, but confinement in a pen did not allow it to leave. After it was a year old, the young male suddenly became very aggressive to both parents, even denying them access to fodder, and the older pair became subordinate. A sibling female matured simultaneously with this development and paired up with the young male and they established new dung deposits. The pen was then subdivided by the keeper and the young male deposited dung along the border netting and continued to threaten the other pair through the wire, but for another fortnight tolerated an eight-months-old sibling male; it then became aggressive to this male

as well, which was put back with the parents. Here, he in turn became aggressive to both parents but courted the mother during her oestrus; furthermore he made new dung deposits along the wire opposite those of the newly hived-off pair. In spite of the artificiality of these conditions, it is interesting that the dominance of an adult over his young one can be reversed and that it is the presence of a neighbour that stimulates dung deposits on a boundary. Before it matures the young appeases the adult male in a very characteristic posture: approaching with both fore and hind limbs bent, it lowers the head and presents the grizzled grey surfaces to view. This creeping posture contrasts strongly with that of an aggressive animal that sometimes need only fluff out its russet crest to send a young animal to flight. The confident high-stepping gait also gives a prominence to the plain warm colour of the legs and the erect posture of the head presents the warm colouring of the crest to view. A curious phenomenon that is common to other neotragines and gazelles is the deposition of secretion from the preorbital glands on to the tips of the male's horns. Both females and subordinate males sometimes place their gland on to the adult male's horn tip and Dittrich (1965) saw juvenile males marking one another in this way. Simonetta (1966) remarks that such marking by a dominant male is excluded because the behaviour is implicitly submissive. Before attempting this dangerous exploit the inferior animal sniffs at the male's gland and licks it. This preliminary possibly conditions the superior in some way to accept the deposit and keep still.

The female ordinarily uses her preorbital glands less frequently than the male and Rainey (personal communication) has noticed that female deposits are placed below those of males. Captive females are more inclined to mark their keepers than males are. The male circulates around his territory at least once a day, spending up to an hour renewing deposits on branches, twigs, grasses and even rocks 20–45 cm off the ground; deposits are scattered throughout the area but are commonest in the most regularly occupied spots. Simonetta remarked that the incidence of a male's markings increases greatly once his offspring have started this behaviour at about five months of age and he also noted that two captive *M. s. phillipsi* assumed threat postures immediately after one had superimposed a deposit on a site used by the other.

Like most other neotragines a conspicuous aspect of their territorial behaviour is the dung ceremony, performed along those boundaries of a family territory that abut with a neighbour. It was mentioned earlier that a captive male established his own dung sites simultaneously with a sudden reversal in the dominance hierarchy, an overnight change in the young male's disposition that has been observed in several captive antelopes. In the wild, the young animal would first be driven off the territory, so there may be a more gradual sequence. Nonetheless, the establishment of dung sites is undoubtedly one of the first acts in the assertion of territory. Simonetta points out that the site for dropping dung may be learned and the behaviour may be partly conditioned; for a mother accompanied by her young goes to the site and after excreting herself induces the young to do the same by licking the genital region. The young soon uses the site without inducement and may even precede the female. The male usually follows close behind,





Madoqua kirkii, female.

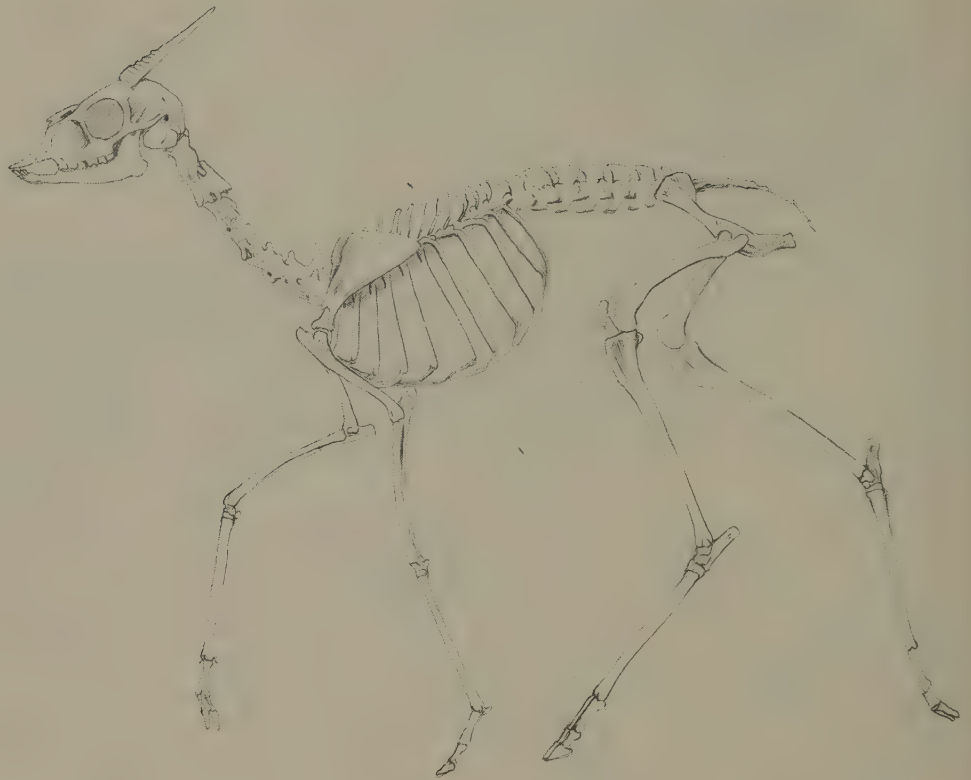
smelling and testing the urine with a tapir-like lip curl. He urinates exactly where she did, scrapes with his hooves and urinates again, followed by more scraping, and then adds his own grain-like pellets—more pointed than those of the female. Of the numerous deposit sites only a certain number are used at any one time but there are periodic changes and new deposits are easily formed. For instance, Hendrichs and Hendrichs introduced dung from completely strange dik-diks into a territory. The dung was sniffed at for a long time and then scratched and superimposed upon. The resultant deposit was regularly visited particularly if more strange dung was about.

The dung of neighbours was ignored completely when strange dung appeared on a border deposit, showing that they can discriminate between individuals on the basis of their dung. Dik-diks may also try to obliterate evidence of other species that have dropped their dung within their territory. I have seen dik-dik activity superimposed on rhino and hartebeest dung, and the latter deposit was also regularly used by a civet cat—it is not uncommon to see viverrid dung added to dik-dik latrines. I have also confirmed Shortridge's observation "A day or two after a herd of elephant had passed through a district where these bucks were plentiful, nearly every elephant dropping will be thickly sprinkled with the tiny pellets of the dik-dik". There is a local folk-tale which parodies the little dik-dik's territorial pretensions. According to the story, a dik-dik one day stumbled over a ball of elephant dung and was so cross that he then always used the same place in the hope that one day it would be sufficiently large to trip up the elephant!

The territory may also be defined by means of sound. The commonest call is a whistling noise which, although uttered by both sexes, is more frequently and persistently made by the male. When dik-diks emerge into open ground to feed in peripheral areas of their territories, often on moonlit nights, these calls are particularly noticeable and they appear to be answered. Likewise, a faked whistle will often draw a response. Sudden disturbances in the territory may provoke a series of bouncing leaps or stotting in which animals whistle as they hit the ground. Their progress usually takes them in a circular direction and is followed by an alert examination of the source of disturbance. The loudest whistle is reserved for certain classes of predator (in which man is sometimes included), but the primary function of the call is probably acoustic advertisement directed at other dik-dik and it seems that any type of alarm whistle encourages a family group to clump together.

Dik-diks squeal when caught and Hendrichs and Hendrichs (1971b) heard a young male pursued by a territorial male squeak, but a lower intensity of fear is expressed by a hiss. Slight disturbances often elicit no more than a temporary alertness and rather breathy wheezes which, like the louder whistles, are accompanied by a sharp downward extrusion of the proboscis.

Another expression of territorial behaviour is the male's vigorous grating of tree trunks with the corrugations on his horns, which fills the horn furrows with vegetable matter. Simonetta noted this behaviour as being especially frequent when the female is in oestrus, at which time the male will seek to approach any source of disturbance, stopping to horn available branches and trunks and sometimes stabbing and twisting as well as grating with an energetic nodding movement. Occasionally the male will break up or somehow pick up a stick with his horns, which makes him nod all the more; this is seen when two males are within sight of one another near their common boundary. Such threats are generally preceded by a high-stepping walk with the head held high and the crest fanned out. When about to come into contact both males stab ferociously at one another but without actually touching; walking back a few paces they advance again and indulge in more elaborate feints. On the whole, wild dik-diks probably avoid clashes but their horns are occasionally broken off at the base in fights and when they fight in captivity the results can be fatal.



Margin: *Madoqua kirkii*; skeleton:
Madoqua saltiana.

Symbolic fights either end in the flight of one participant or just peter out in desultory poking at vegetation followed by a dung ceremony. It is interesting that the aggressive posture displays the warm-tinted neck and legs to the opponent and that a territorial male advertising his presence by standing around in the territory also arches his head back so that the throat is exposed and the back of the neck and shoulders disappear in the bunched posture (see drawings).

Territorial behaviour reaches its peak over the female's oestrus and it is evident from captive groups that she elicits great interest from any male with access to her.

What factors are responsible for seasonal breeding are unknown. Kellas (1955) noted that the rise and fall of solar radiation corresponds with the peak of sexual activity preceding the solstices. Tinley (1969) believes that nutritional fluctuations might be responsible, but Hendrichs and Hendrichs' (1971b) study has shown that the protein content of their dry season food is very high and dik-diks are probably able to sustain a rich year-round diet. Both Kellas and Hendrichs thought, however, that cover for the newborn was an important proximate factor. In this connexion it would be very interesting to compare the survival rates of young born at the beginning of the wet season with those born at the beginning of the dry.

The forming of a pair in a captive group has already been described. Hendrichs and Hendrichs reckon that an evicted female finds a place to settle and awaits a young male or alternatively joins any male that might be without a mate.

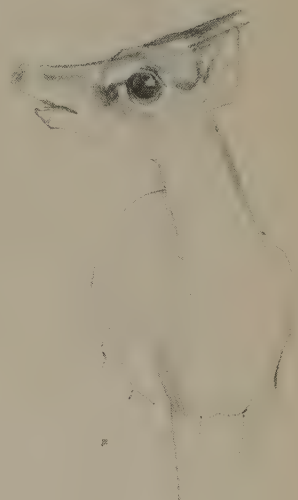


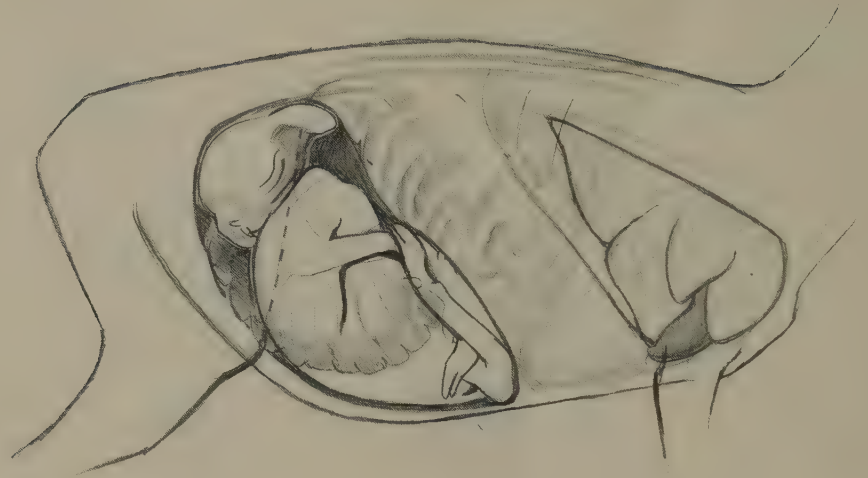
Madoqua guentheri.

Courtship is very distinctive: the oestrous female appears somewhat dazed, her movements slow down and she keeps her nose raised while she walks near the male. Sometimes she reveals a circular ruff of brilliantly white hair on each haunch and her minute raised tail flicks slowly, and it appears that this highly conspicuous signal is a strong stimulus for the male. Like the young, the female may produce a drop of urine on being licked by the male but this is by no means invariable and it is perhaps water economy that has encouraged the development of a vivid visual signal to advertise her condition. However, Morgan Davis (personal communication) has seen the male also expose his white rump-flag while copulating and I have seen a shot male make an involuntary rump display at the point of death. Another indication that urine testing might be less important for the dik-dik than other antelopes is its optional occurrence in the courtship ceremony; males may dispense with the lip curl altogether or they may apply the nose to dry genitalia; *flehmen* itself consists of a brief wrinkling and lifting of the proboscis.

The first preliminaries of courtship focus on the facial region, with the male sniffing and nuzzling the pre-orbital gland, after which he turns his attention to the doe's vulva. Copulation may be preceded by some chasing. Simonetta noticed that while the female was in oestrus, a disturbance that brought male and female close together could cause a rapid switch from alarm to sexual behaviour. For the two or three days she is in oestrus the female is constantly attended.

Madoqua kirkii.





Full-term foetus of *Madoqua*, *in situ*.

Gestation lasts 170—174 days, a male fawn weighs 725—795 g and females weigh 560—680 g at birth (Hendrichs and Hendrichs, 1971b). Post-partum oestrus occurs about 10 days after the birth, so that mating and parturition take place at much the same time of the year. The female, therefore, is pregnant most of the year and lactates for about six weeks, once in the rains and once in the early dry season.

The female stays with her young for the first day following its birth, with frequent short absences to feed but she soon leaves it for longer periods until she is only visiting it four times in the 24 hours, at sunrise, about midday, at dusk and at midnight. Although the mother may remain with her young up to a quarter of an hour, suckling is completed in a minute or two. The young one is contacted by means of a call, which is presumably ultrasonic, as the muscular effort of the proboscis that is made in conventional whistling is evident but the sound is inaudible to the human ear; the young one responds at once by emerging from its refuge to suck and be groomed. After a short frolic the fawn returns to its hiding place or is led to a new one by the mother. Any sudden scare elicits crouching and freezing, and during the first week or so the parents themselves often cause this reaction, in which case they come and nudge the fawn into activity. If frightened, it makes a squeaky bleat. During the day the young one is silent, but it may whistle at night.

Both parents have intimate contact with the young animal and the male will groom the juvenile when it approaches him, licking its back, neck and muzzle. Simonetta noted the male interrupting its browsing or ruminating to join the young whenever it emerged and the growing youngster often chose to rest beside the male. When Simonetta approached a shelter occupied by a family, the male took flight first but it kept converging on the source of danger whistling all the while. When Simonetta got still closer, the mother and finally the fawn bolted.



Juveniles indulge in mock fights and Ziegler Simon (1957) records a captive female challenging people, dogs and turkeys.

By the age of three weeks the birth weight has doubled and by the age of eight months the fawn is of adult height but it does not achieve adult weight until it is one year old.

Females may be mated at about ten months and males have been seen to copulate at the age of nine months.

Hendrichs and Hendrichs have estimated that 50% of the fawns survive while 10—20% of the adults are lost each year. On this basis, if territories are held between five and ten years, the population will remain in equilibrium.

Although hunted widely in East Africa, dik-diks have probably been favoured in the short term by ecological changes wrought by overgrazing and by the fallow and disturbed vegetation that accompanies human expansion (see Vol. I, p. 41). They are fairly easily netted and Simonetta describes Somalis actually running them down by persistently chasing them round their territory. The skins are sold for karosses and for fine glove-skin suede.



10

opening and
closing of mouth

Harry
Lester
Ward

7. 10. 1911.

Duikers

Cephalophini

Genera

Cephalophus 12 species in East Africa

Sylvicapra one species

Throughout the forests of the world but particularly in the tropics there are medium-sized terrestrial herbivores that live inconspicuous existences in the undergrowth. In Asia and South America there are cervid genera such as *Muntiacus*, *Mazama* and *Pudu*, while the rodents *Cuniculus*, *Myoprocta* and *Dasyprocta* have filled similar niches in the Amazonian forests. In tropical Australasia there are marsupial wallabies, *Dorcopsis* and *Dorcopsulus*, while the African forests are dominated by neotragine and cephalophine Bovidae. Some of these remarkable convergences have been described by Dubost (1968), who pointed out the common physical characteristics of low-slung bodies on slender legs and wedge-shaped heads with relatively large eyes. He also noted that the African duikers have radiated to fill a variety of special biotopes while remaining predominantly adapted to high

Opposite: *Cephalophus harveyi*.
Below: *Cephalophus monticola*.



forest. Dubost's observations of convergence in the body build of totally unrelated groups implies not only a very powerful discipline exerted by the forest habitat but their adaptation is often so specific as to inhibit their colonization of other habitats and, indeed, only one duiker species, *Sylvicapra grimmia*, manages to live in relatively arid habitats. The absence of great variation in the basic form of these antelopes suggests that their morphology represents an exact and well-tried adaptation. *Cephalophus* is the most widespread of forest antelopes and also the most thoroughly tied to moist shady habitats.

There is no indigenous forest in Africa without at least one species of duiker and the existence of 18 species of *Cephalophus* is in the first place some indication of their importance and success as a dominant forest antelope but, since many of these are allopatric, it is also a measure of the fragmentation of the African forests.

The profile of this genus will explore their diversity through a discussion of distribution and speciation. On the other hand, this profile will discuss the origins of the group and stress their common features, for it is the homogeneity of duiker species that stands out when comparisons are made with other antelopes and this suggests that their radiation is relatively recent.

How did duikers evolve? A complete absence of any useful fossils means that we must rely on comparative morphology for clues to their origins. I believe that this can be deduced and I consider that many features of cephalophine behaviour, ecology and anatomy are compatible with their derivation from a dwarfed neotragine stock.

The ancestral neotragines were probably predominantly herbivorous and I have already made the point that a scarcity of herbage on the forest floor would have been one of the original determinants of diminutive size. In the context of duiker evolution neotragine dwarfing can be regarded as the mechanism whereby a relatively advanced herbivore coming from outside Africa could invade the equatorial forests and make the necessary adaptations to an environment and microclimate that was radically different to the savannas and woodlands outside.

Once this environmental adaptation had been made a new avenue of evolution opened up for the dwarf antelope. The forest floor offers an abundance of fallen fruit, fungi and invertebrates for a small animal with a less restricted diet and I consider that a secondary dietary reversion back to a more omnivorous diet may have precipitated the morphological changes that today distinguish *Cephalophus* from *Neotragus*.

Perhaps the most radical anatomical differences between these genera concern the closely associated frontal and nasal bones. In *Neotragus* the frontals form a broad concave plane, in *Cephalophus* this is long and convex in shape. In *Neotragus* the horn arises from above the orbit whereas in *Cephalophus* the bud has migrated with the backward movement of the frontal bone to a position near the top of the braincase. In *Neotragus moschatus* the nasals are relatively flat, straight-sided plates, in *Cephalophus* they are curved with irregular sutures along their margins (and a particularly deep expansion between the lachrymal and the maxilla). There is also an overall thickening of the bones and tighter knitting of the sutures even in the smallest of the duikers. The edges of the duiker's preorbital fossa are

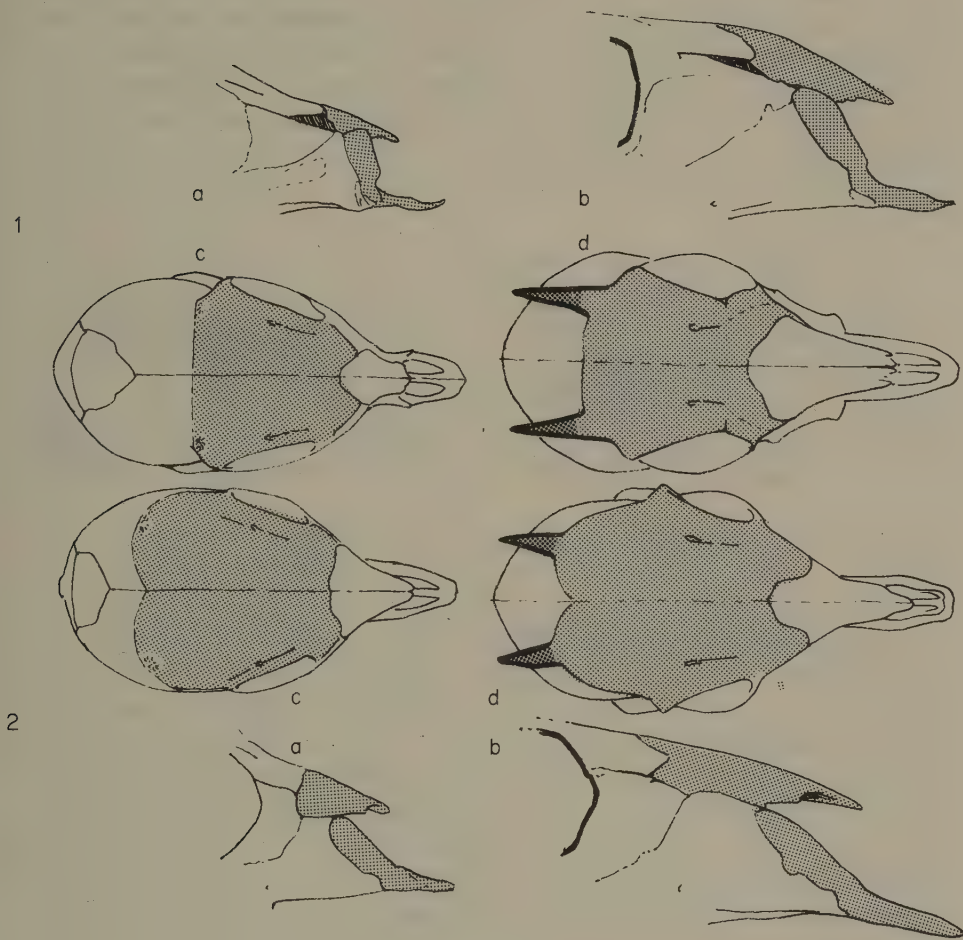
Cephalophus callipygus with section cut out of forehead to show thickness of frontal bone (13 mm at thickest point).



softly rounded instead of sharp-edged (this can be correlated with a smearing technique of glandular marking instead of precise insertion of twigs into the gland). The ducts of the gland have a series of small surface openings instead of draining into a single orifice.

Finally, cephalophine brains are appreciably larger than those of neotragines and this might influence the bulging paedomorphic forehead that is so characteristic of duikers.

If the duikers condition is derivative, as I propose, it is necessary to consider how such changes could have taken place.



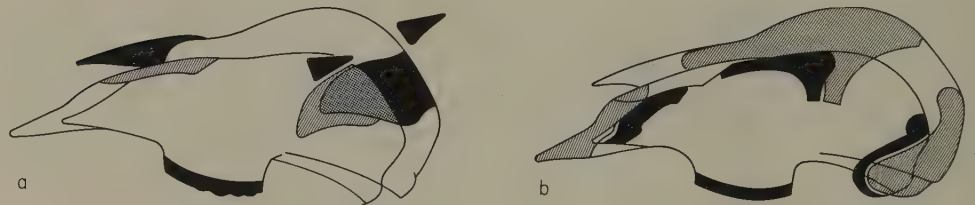
Frontal bone, nasals and premaxilla in *Neotragus* spp. and *Cephalophus monticola* 1a, b: side view of the muzzle in neonate and subadult *Neotragus pygmeus*; 1c: dorsal view of neonate *Neotragus pygmeus*; and 1d: adult *Neotragus batesi*; 2c, d: dorsal view of neonate and adult *Cephalophus monticola*; 2a, b: side view of muzzle in neonate and adult *Cephalophus monticola*; 2a, b: side view of muzzle in neonate and adult *Cephalophus monticola*.

A flatter angle and shorter length of horn can be correlated in the three species of *Neotragus* with diminishing size (see p. 176) and it is likely that the relative importance of these weapons is reduced as body weight and build become lighter. I have already observed that *N. moschatus* use the flat shaft of their horns to administer butts or glancing blows (p. 198). In the smallest species, *N. pygmaeus*, horn fighting is probably less frequent and the very short horns lie so flat that their origin over the orbit can only be described as anachronistic as the tip alone is free from the skull's surface and the brunt of butting would have to be taken directly on to the forehead.

If I am correct in viewing the pygmy antelopes as scarce relics derived from once abundant, widespread and ecologically less restricted populations, it can be predicted that densities would have been higher in those populations that had modified their feeding habits to make better use of the resources of the forest floor. Yet if one is to judge by the very small size of horns in some relatively large species of duiker, it seems likely that the ancestral cephalophines had horns that were more vestigial than in *N. pygmaeus*. This is given further credence by the duikers' normal fighting technique which is a blunt stroke with the forehead.

Only vestigial horns could have been as radically displaced as they are in *Cephalophus* but the process might have been facilitated in a dwarfed, nearly hornless form where the structural considerations centred less on the horns than on the frontal bones. These bones would have had to respond to enlargement of the brain and to the tests of intraspecific competition (in other words, external battering) while they might also have been involved in alteration of the basi-cranial axis.

Superimposed skull outlines of *Neotragus batesi* and *Cephalophus monticola*: a. three areas in which there are minimal differences in the dimensions, i.e. nasals, parietal and toothrow; b. three areas in which there are maximal differences in the dimensions, i.e. frontal, occipital and bullae, premaxilla.



The horns' migration, therefore, seems to have been an integral part of a profound perturbation and backward expansion of the frontals. If the horns of *Cephalophus adersi* are compared with those of *N. pygmaeus* it could be said that the position of the former is a "rationalized" equivalent of the latter in that the non-functional, orbitally rooted stem has been eliminated and replaced by a robust bony pate. This cranial shield is continued down the bridge of the nose to the nasals. The cephalophine condition is actually anticipated in the two smaller *Neotragus* species in their tendency to form tight bonds with the lachrymal and premaxilla and in their curvature, but advanced duikers are unique in having nasals that actually wrap round the tube enclosing the upper turbinals.

The fundamental structure of the preorbital gland is similar in both Neotragini and Cephalophini (Hofmann, personal communication). This complex of secretory cells drains into a single large invagination in most of the Neotragini. This orifice is reduced in *N. batesi* and is so minuscule in *N. pygmaeus* that no twig could possibly be inserted and Owen (1973) was unable to express any secretion from it in a tame female. In a year of observation this animal was never seen to use its gland for marking, but it resembled duikers in that it closed its eyes when the gland was rubbed and solicited more stimulation with nudges after the rubbing stopped.

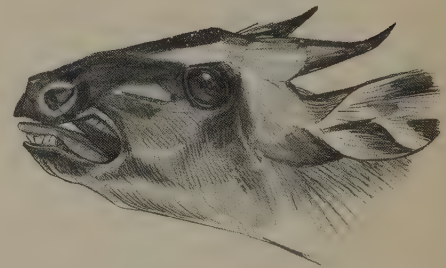
Differences in tooth structure are as great within the genus *Cephalophus* as between some of the *Neotragini* and *Cephalophini* but, in correlation with the difference in diet, duikers' molars tend to be broader and the inner cusps have their margins more bowed than angled. The palatine bone tends to be slightly more reduced. That feeding habits may have a relationship with the size of the neocortex has been suggested by Oboussier (1979) and the demands of a varied diet (including vertebrates and insects) may have influenced the development of large brains in the duikers. Haarmann (1972) determined that the cephalophine cortex is thicker than in *Neotragini*, while greater space between pyramid cells implies more connecting cells. Noting the deep cephalic sulci and high brain-bodyweight ratio of duikers, Oboussier (1979) concluded that, although neotragines have a very similar cranial morphology to duikers, the former have less evolved brains and that the *Cephalophini* are not a primitive group. Greater similarity between the sexes is also apparently linked with higher brain evolution. I think it is also most likely that an altered ratio between brain and body size was one of several allometric growth gradients that were associated with the dwarf phase of duiker evolution.

The smallest of living duikers, *C. monticola*, is the most widely distributed and one of the most abundant of all forest duikers. Nonetheless it is appreciably larger than the pigmy antelopes and its monopoly of the small forest duiker's niche may explain the absence of more primitive linking types. The ancestral duikers were probably below the optimum size for a ruminant (Janis, 1976) and may eventually have been subjected to decisive competition not only from larger descendants but from other small omnivores.

Duikers have an unusually large mouth and wide maw and this is seen to best advantage when they feed on large fruits, which may be picked up and juggled about in the mouth with the nose pointing up in the air. Alternatively, with a heavy fruit, an exposed root or bark, they may retract their lips so that the sharp saw-like cheek teeth can directly cut away these tougher foods. Delicate herbs and shoots are pulled with the lips alone while tougher herbage is also wrapped by the long pointed tongue and yanked over the incisors' cutting edge. The limited but varied foods of the forest floor probably encourage opportunistic feeding habits and animal foods are often taken by all species; the suggestion that small birds and mammals are killed by captive duikers to compensate for an artificial lack of salts is vitiated by the presence of insects and meat in the stomachs of animals shot in the wild. This subject is worthy of further investigation, particularly in the light of Aeschlimann's observation (1963) that the digestion of a pigeon eaten by *C. dorsalis* was quite complete.

Hofmann (1973) found that the duiker stomach is well suited to rapid absorption through the richly papillated mucosa of the ruminoreticulum. He thought it doubtful that duikers could exist for long on a grass or roughage diet. Salivary glands are of exceptional size (see dissection p. 263). Feeding is often conducted rapidly with long spells of rest or rumination in between but activity patterns probably vary from species to species.

The resources in closed canopy forest consist of rather few shade-loving plants at ground level, fallen fruits, seeds and flowers, shoots, leaves and



Cephalophus nigrifrons.

Forest type	Lowland Forest closed, high canopy, thin undergrowth	Lowland and montane forest, broken canopy, dense undergrowth	Alpine and subalpine habitats	Swamp forest	Gallery , riverine and drier , low canopy forests	Forest edge and secondary growth
Main food resources for duikers in possible order of importance	Fruit, shoots and seedlings, leaves , flowers, bark and fungi	Fruit and herbaceous growth , leaves, shoots and seedlings, fungi	Herbaceous growth, leaves, fruit, moss, young grass	Fruit, herbaceous growth, fungi, bark, semi-aquatic vegetation	Fruit, leaves, seasonal shoots, seedlings and herbace- ous growth	Fruit, herbaceous growth, shoots and seedlings
SPECIES						
<i>C. silvicultor</i> 68 (45 - 80) kg		mainly nocturnal (in Gabon 71% fruit 29% leaves)				
<i>C. spadix</i> 55 (52 - 60) kg		allopatric sibling sp. of above (montane only)				
<i>C. dorsalis</i> 22 (14.5 - 24) kg		Nocturnal. In Gabon 73% fruit 27% leaves				
<i>C. callipygus</i> 20 (16 - 23) kg	Diurnal. In Gabon 83% fruit 16% leaves					
<i>C. nigrifrons</i> 17 (13 - 18) kg		Diurnal. In Gabon 72% fruit 28% leaves				
<i>C. harveyi</i> 15 (13 - 16) kg		Diurnal. and nocturnal			Diurnal and nocturnal	
<i>C. rubidus</i> 15 kg			Diurnal			
<i>C. leucogaster</i> 13 (12 - 18) kg		In Gabon 73% fruit 27% leaves and flowers			Diurnal	
<i>C. rufilatus</i> 13 (12 - 14) kg					Diurnal and nocturnal	
<i>C. natalensis</i> 13 (12 - 14) kg					Diurnal and nocturnal	
<i>C. adersi</i> 8 (16.5 - 12) kg					Diurnal	
<i>C. monticola</i> 5 (3.5 - 9) kg	In Gabon 78% fruit 20% leaves				mainly Diurnal	

Distribution of forest duikers according to habitats with main food resources indicated. Dietary data from Gabon after Gautier-Hion, Emmons and Dubost 1980

branches dislodged by wind and the activity of monkeys, rodents, bats and birds. Seeds that are not eaten germinate continuously and the entire forest floor is a seed bed for struggling saplings; then there are also the barks of various trees and exposed roots. Fungi are abundant in places. On steep hillsides or wherever the canopy is broken by a fallen tree, sunlight encourages a dense tangle of undergrowth that is temporarily within reach of terrestrial herbivores. In the glades or along river banks and forest edges there is a less transitory growth of herbs and sedges. These then are the principal vegetable resources on the forest floor and all are eaten by the duikers. Where there are tangles of fallen branches some of them can, like goats, balance on their hind legs or clamber up and over the boughs to reach leaves or fruit nearer the sun, but they normally depend on food within one metre of the ground and as this may be scattered rather unevenly through the forest, the duikers too tend to be more abundant where these resources are greatest.



Skeleton of *Cephalophus callipygus*.

Although all duikers feed on a similar assortment of foods, Dubost (1980) has provided some evidence that the relative importance of the items varies from species to species. This has some correlation with variations in the type and abundance of foods in the different habitats; in the accompanying table I have attempted to sketch out this aspect of ecological separation, ranking the major food resources according to their possible importance or abundance in six habitats. Because nocturnal or diurnal habits may help keep species separate, I have indicated the predominant activity periods of the species listed.

Other factors that might be relevant are the relative mobility or extent of range, breeding rates and tolerance for differing levels of competition or predation, while behind the feeding and activity regimes of individual species there may be specific physiological refinements. As far as is known all species space themselves out in territories. The size of both the duiker and its home range must be related to the year long supply of food and much interesting work could be done on correlating these elements in both specialized and unspecialized duiker species.

Some of the evolutionary implications of a size gradient in duikers are discussed in the next profile. The smallest species, *C. monticola*, tends to occur throughout the forests while the largest species, *C. sylvicultor*, only concentrates in areas where plentiful secondary growth will support such large beasts. The majority of species are in the middle-size range. Observation of the animals and their traces confirms that most species have relatively small home ranges, although short-range seasonal or daily peregrinations have been observed in some species (see *C. nigrifrons* and *C. sylvicultor*). Hofmann (1973) reckoned that a pair of *C. harveyi* near Nyeri lived for four years within an area of about 12 ha but he thought that animals living on the Kikuyu escarpment might have a more extensive range. There are well-trodden and regularly used pathways connecting their habitual feeding, ruminating and sleeping areas, and the male constantly renews glandular marking posts and stands or rests at certain definite stations, all of which illustrate that territorial behaviour is well developed and that the home range is known intimately to its occupants. It has been suggested that they might advertise their territory acoustically, as the imitation of a bleat will call up duikers in the vicinity, (a ploy that is effectively used by some traditional forest hunters). However, adult duikers also respond to a distress signal.

Duikers are difficult to study because their senses are generally more acute than those of would-be observers. When they see an intruder they will either freeze in a standing position or, if they are young, will lie down and stick tight. If an approach is detected well in advance, the duiker will deliberately move into a thicket or move over and keep hidden behind a tree.

Dubost (1968) described *C. dorsalis* seeking out the hollows of fallen tree trunks to rest in and I have found them sheltering in the dark caverns formed by tree buttresses, I have also noticed a difference between species in their choice of resting stations. *C. harveyi* almost invariably ensures that there is a low canopy overhead and often keeps a clear view all round. Both *Sylvicapra* and *C. sylvicultor* on the other hand, are mainly concerned to have a solid background and tend to rest with their backs close to a tree trunk, termillary, bank or dense thicket. A skilled selection of hiding places is made by the young almost immediately after birth and slightly different factors clearly influence the choice made by each species. Some species' territories are shared by a male and a female and, although they are usually within reach of one another, the male is more active, patrolling and marking his territory daily.

Observations on a pair of *C. harveyi* kept in a one-hectare enclosure suggested that the male might have rather different activity cycles to the females. He would circulate the area and take a series of stations for periods of an hour or so, lying down and ruminating or simply standing. The female was attached to fewer resting spots, which she sometimes shared with the male but there was never any hint of self-display in her behaviour.

It is possible that females of those species in which both sexes have equally long horns are more territorially active, particularly towards other females trying to enter their territories, such territories could be relatively independent of the males.

Ralls (1974) studying *C. maxwelli* in captivity found that social encounters between different groups always involved glandular markings. Indeed, any new object in the territory is marked with the glands and females also mark vigorously if introduced to a strange female. These captives were kept in artificial groups of three, but one of the females always seemed to play a very neutral role, showing no response to strange duikers and seldom grooming the male, so that of each trio it could be said that only one of the females was paired up with the male. Ralls noticed that the secretions from the female's facial glands became transparent like that of the male when she was pregnant but became bluish again after she had given birth. In both sexes the glands' size grows and shrinks and can become grotesquely large in the males. Judging from a large series of duiker skulls, the bony depressions into which the glands fit seem also to vary greatly. It should be borne in mind that even the formation of this bony structure might be influenced by the glands' activity, which is presumably under hormonal control.

All duikers spend much time grooming one another's head and shoulder region but most especially the forehead tuft. Ralls recorded that a male *C. maxwelli*, would normally initiate the grooming (82% out of 600 grooming bouts) but that the females very seldom groomed one another (8%). Grooming has two components; one is licking with the long tongue, the other is vigorous nuzzling with the broad bare rhinarium. Obviously the texture and the surface to be groomed must provide a strong tactile stimulus

	Marks per ten minutes		
	In own group	After male visit	After female visit
Male	6.6	15.2	6.1
Female	3.5	3.7	18.6
Subsidiary female	0.06	0	0.09

Mean number of marks with maxillary (preorbital) glands by *Cephalophus maxwelli* (from Ralls, 1971).



Cephalophus adersi.

and the differentiation of duikers seems to have taken account of this (see the next profile). The facial region, the rump and sometimes the feet are marked with rather discrete signal patterns, most particularly the forehead tuft and the ears. The rough-necked duikers have sharply contrasting lips and chins which appear to flag while the animal ruminates, but the chin and its pattern probably also play a role in mutual grooming and in courtship when faces are repeatedly rubbed together.

The tail flag is perhaps most striking in *C. monticola* where white hairs in the flickering tail appear to enhance and reflect light and contrast strongly with the very dark rump. In this species the tail can sometimes look like a little torch being switched on and off in the forest twilight.

When duikers aggregate in groups larger than a family of three, it is probably at water, a salt-lick or at a fruit fall near two boundaries. Bourlière and Verschuren (1960) saw six *C. sylvicultor* together and *C. natalensis* are not infrequently seen in temporary aggregations of similar size.

Sikes (1958) reported that captive male *Sylvicapra* were especially intolerant when the female was in oestrus. Fights between males are preceded by very vigorous marking and horn thrashing against the marked spot with twigs and saplings sometimes broken and tossed in the process. The males face up with the forequarters held low and they often drop on to their knees when clashing. However, it would seem that every animal tends to stick to its own well-marked area. Seasonal movements are known to occur in some species but they probably involve two rather limited traditional areas. In Bwindi forest, *C. nigrifrons* move down from very dense tangles at higher altitudes to feed nearer the rivers and, although this is a daily movement, it is apparently only of seasonal occurrence.



Cephalophus callipygus.

The courtship of duikers shows similarities with that of other antelopes in that the male lip-curls over the female's urine and strikes out with his foreleg. The male urinates with the body stretched while the female adopts a hunched posture. There is usually a long circular chase in which the male of some species repeats a bleating call. The male sometimes struts on tiptoe, trying to maintain a lateral presentation and approach closer at the same time, with the result that he performs a manoeuvre like a dancing circus horse. Continuous face rubbing seems to have almost narcotic effects on the female.

As has been mentioned, the young hide themselves after birth but emerge at the mother's call. They have a surprisingly strident bleat. The female wipes her gland all over the young soon after birth and in grooming she

renews the marking. Heinichen (1972) heard a mother *C. natalensis* make warning calls when an intruder approached the newborn fawn. Duikers are known to have lived up to nine years in captivity.

Duikers are a common prey of leopards, golden cats, pythons and the large hawk-eagles but their principal enemy is man. They are particularly vulnerable to being netted and snared and a slight acquaintance with an area soon reveals regular flight paths. Their response to calls has already been mentioned and this is exploited by hunters in many forest regions.

The ecological separation between different species of *Cephalophus* is discussed in the next profile. Competition with other ungulates is difficult to assess but the bushbuck is a common cohabitant and potential competitor of most species, although dietary overlap is only partial. An interesting fact related to this has been revealed by wildlife extermination campaigns in Rhodesia and Uganda. The killing of all the large ungulates over extensive areas makes for more cover and perhaps more food for *Sylvicapra* and it also seems that the bush duiker manages to keep pace with quite a high rate of slaughter without any drop in numbers. This is discussed further in the profile of that species.

Cephalophus

Duikers

Species

Cephalophus adersi
Cephalophus natalensis
Cephalophus harveyi
Cephalophus nigrifrons
Cephalophus rubidus
Cephalophus rufilatus
Cephalophus leucogaster
Cephalophus callipygus
Cephalophus spadix
Cephalophus sylvicultor
Cephalophus dorsalis
Cephalophus monticola

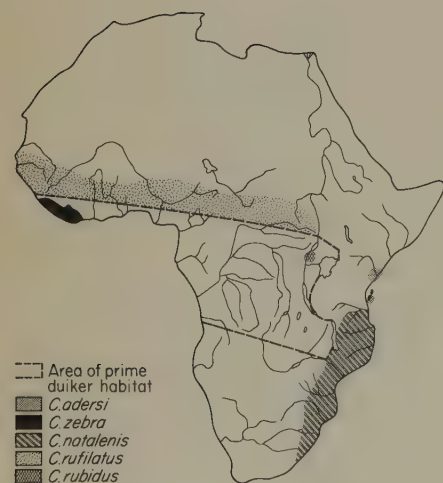
A striking peculiarity of this genus is the existence of many distinct forms without any great departure from a basic body plan, except in one particular—size.

That dimensions are of immediate ecological significance is shown by the fact that duikers coexisting in the same area of forest are generally of different sizes. There is also an ecological separation of species that is most clearly demonstrated by altitudinal zonation on mountains and adaptation by separate species to secondary growth, forest edges and to swamps within or outside the forest. It should be stressed, however, that in no case has the morphology of a species been greatly modified to accommodate to such specialized habitats. Duikers inhabiting dry thickets, alpine screes and swamps resemble those living in true forest and are closely related to them.

There are peculiarities of form that imply unknown adaptations in some little known West African species, i.e. *C. zebra* (with an armoured skull) and *C. ogilby* but it should be noted that these belong to a community of very numerous duiker species.

In spite of its forests being peripheral, eastern Africa has a special relevance for an understanding of duiker evolution because of the existence of several generalized species which do not exist in the complex and competitive communities further west; some of our duikers may therefore be the survivors of once more widespread species. As I remarked earlier (Vol. I, pp. 71—76), East Africa's small and fragmentary forests probably shelter representatives of a succession of faunal eras. In fact, as one travels east the degree of isolation from the main forest block is sometimes a measure of the age of the fauna inhabiting it; thus the southern Highlands, the "Mozambique zone" and Zanzibar are three such age-graded regions, each sheltering a different and successively smaller red duiker.

Excluding the "specialists" only two or three (strictly size-graded) species are really common within the lowland tropical rain forests. These



Distribution of the smaller red duikers. Note that all have peripheral or relict distributions or have specialized habits.

are the "main line" species that dominate the primaeval habitat of the genus today; yet the largest species are likely to be among the more recently evolved (see Vol. II, pp. 70—72).

The smallest species, the little blue duiker, *C. monticola*, is the most widely distributed of all forest species, even occurring on several oceanic islands. By contrast, the dwarf red duiker *C. adersi* is a rare and localized relic (see Vol. I, pp. 8, 12, 71—75). Both these small duikers are probably relatively ancient but *C. monticola* is phylogenetically isolated, being the only duiker with a sharply pointed muzzle, reduced premolars and other peculiarities, whereas *C. adersi* belongs to the group that includes all the dominant species.

The duikers resemble the other bovid lineages in showing a progressive trend towards larger size but the small range of sizes could reflect both a diminutive ancestral stock, recency of evolution and a limiting food supply. The distribution pattern of the very numerous forms across the forests of Africa and a complex of ecological displacements or equivalences between the species suggests that the broadest outline of their evolution can be reconstructed. It is clear that the diversity of duikers is the manifestation of a complex radiation but each species is such a mosaic of characteristics that a variety of groupings and relationships can be postulated. Attempts at defining relationships within this group have been made by Schwartz (1920), St Leger (1936), Heyden (1963), Haltenorth (1963), Ansell (1968) and Groves and Grubb (1974). Each of these authors grouped species together in a different arrangement.

It is easy to misjudge the affinities of a distinct form but apart from the likelihood of error that is inherent in lumping duikers it is important to recognize that populations may also be representative of different evolutionary levels. This gives a special value to the definition of distinctness (see Vol. I, p. 5).

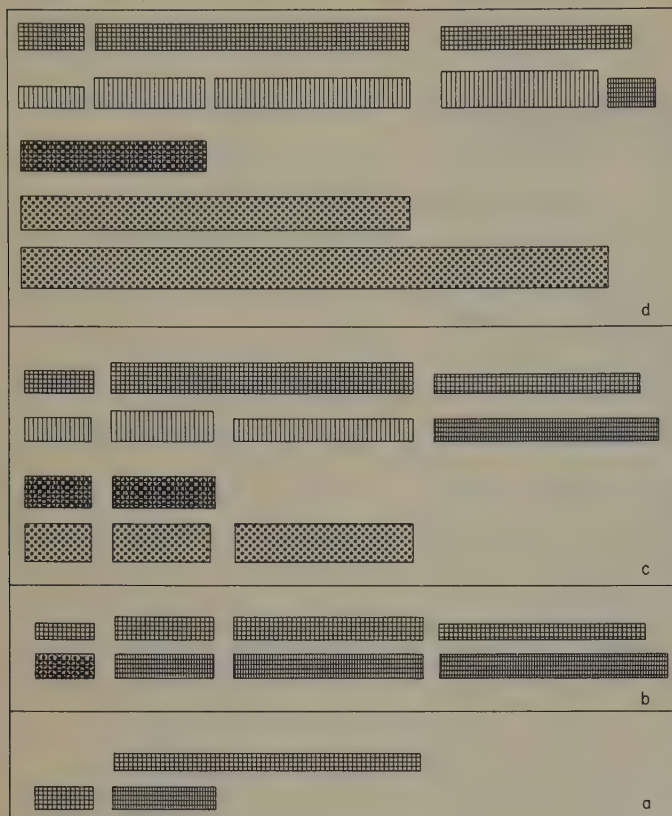
I have preferred to draw attention to the complexity of evolution in *Cephalophus* by using 12 specific names rather than obscure it with contrived lumpings. At the present stage of knowledge I think this simplifies the discussion of affinities without prejudging them.

My preliminary interpretation of the duiker radiation assumes that repeated oscillations of the forest refuges have provided the mechanism for an evolutionary advance which is most crudely traced as a step by step progression towards ever greater size.

Their distribution suggests that the line best represented in East Africa may have been overtaken in the most favourable habitats by a mainly West African group that is generally larger in body size. The first, which contains the most numerous species is characterized by long, generally coarse fur on the neck and shoulders. Isolated species inhabit all forest types in eastern Africa but in central and western Africa this group tends to be restricted to specialized habitats.

Duikers belonging to the second lineage can be identified by their smooth, short-haired necks. This group includes the commonest large species in the main forest block and the more widely distributed giant duikers.

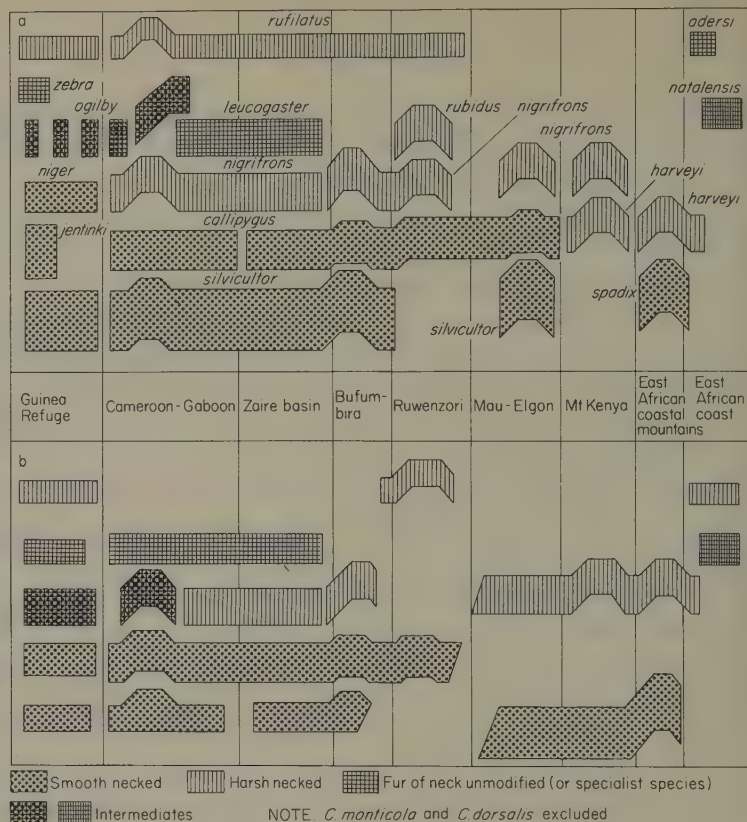
The deviation of two otherwise very similar duiker groups over an



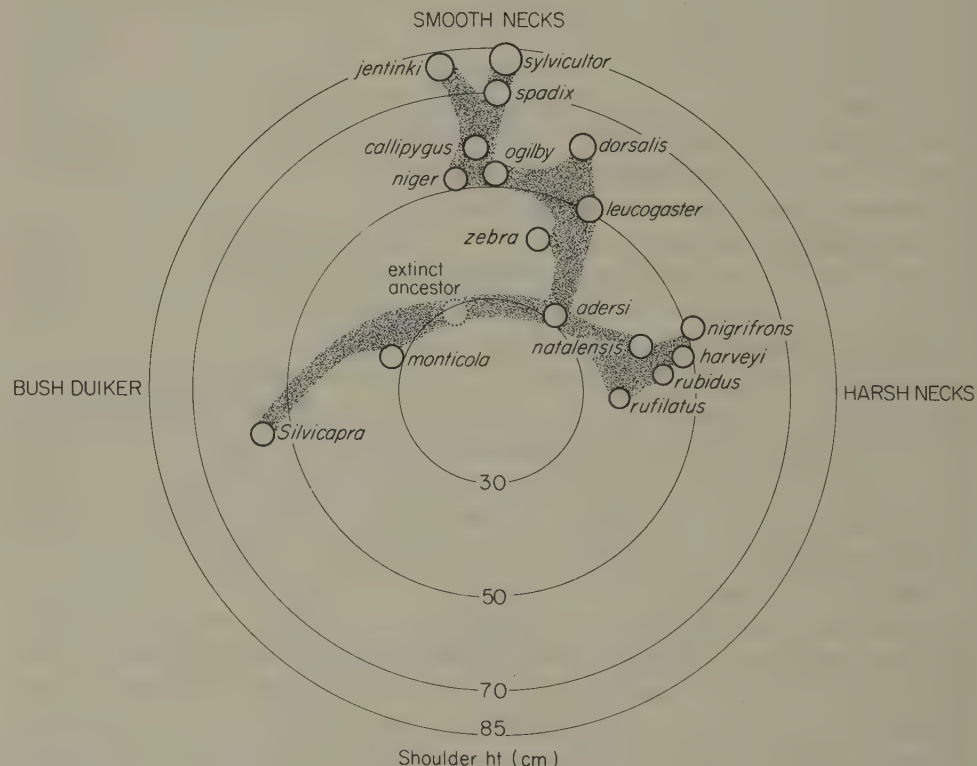
Above right: a. Contemporary distribution of red duiker populations. Width of bars suggests relative size of species. Length of bars suggests extent of distribution (see maps). Montane stratification suggested by kinks. Note: *Cephalophus monticola* and *Cephalophus dorsalis* excluded.

Above right: b. Schematic distribution during earlier period (with *Cephalophus rufilatus* and *Cephalophus sylvicultor* in hypothetical centres of origin).

Above left, reading from bottom to top: successive changes in populations of red forest duikers in tropical Africa. Progressive increases in size indicated by width of bar. Gradual proliferation of types through repeated isolation and rejoining of forest belts indicated by breaks and extension bars. Divergence in texture of neck fur indicated by hatching and stipple. West African centre for (later) evolution of smooth-necked duikers shown on left. Central Africa as centre for earlier evolution of harsh-necked duikers shown centre. Role of East Africa as repository for relic forms suggested shown on right.



Bottom right: Schema of hypothetical relationships among Cephalophini. Note that in the radial dimension scales used to denote size differences and relative phyletic distance are regarded as equivalent. Hatching suggests approximate evolutionary connexions.



apparently minor characteristic, the texture of the neck fur, is of some significance, since the contrast is generally less noticeable in outlying duiker populations whereas the difference is extreme in most of the sympatric species. Because neck grooming is a conspicuous activity of bonded pairs, this development has presumably helped to discourage interbreeding (notwithstanding evidence that hybridization between coarse and smooth-necked duikers may actually occur in the wild).

This arrangement can be compared with the distribution of duikers according to refuges, which can be rendered in a diagrammatic format with species listed by name and altitudinal zonation on mountains indicated by small peaks. This should be compared with the distribution maps.

To explore the size factor in the radiation of species I have used a radial convention (opposite), which places symbols for the smaller species nearer and symbols for the larger further from the centre, while their relative proximity suggests degrees of possible affinity.

According to my interpretation the smallest species, *C. adersi*, might provide some indication of the earlier origins of all the red duikers types because, although not close to any other species, it does provide some sort of a link between the two major radiations. This generalized species has a relic distribution on Zanzibar Island and the Kenya coast. It has peculiar colouring but the fine silky fur scarcely differs in length or texture from neck to body; it has an all-red coronal tuft and a marked cow-lick on the nape.

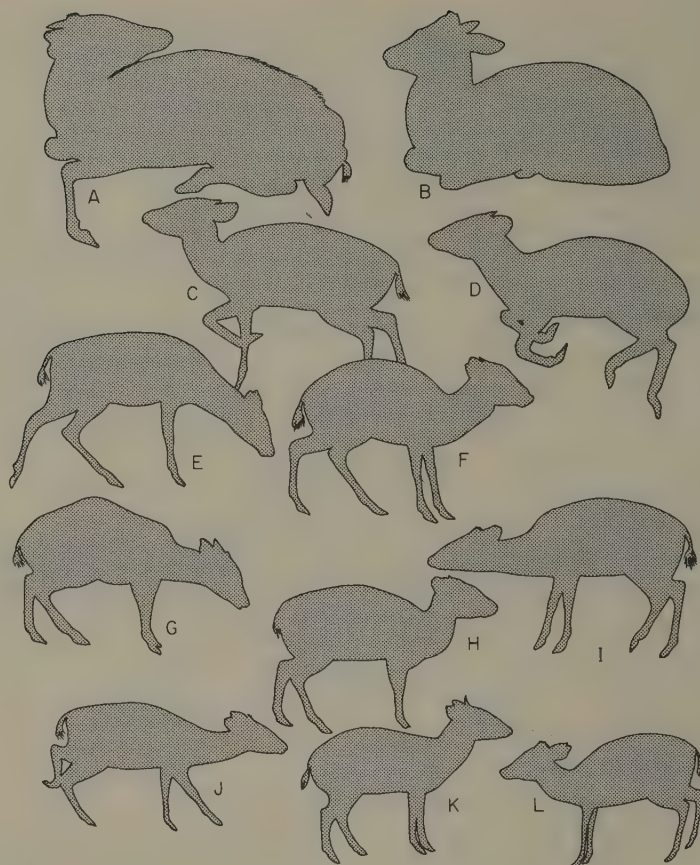
The other small red duikers, *C. zebra* and *C. rufilatus*, are aberrant coarse-necked species and cannot be easily compared with *C. adersi* except in size. Unlike the latter, neither is far removed from the centres of duiker evolution and they can be assumed to have evolved interacting with numerous other duikers. If small size is an attribute of age in duikers and adaptation to special niches requires competitive pressure from more advanced forms, both *C. zebra* and *C. rufilatus* might represent the modified survivors of relatively early phases in the red duiker radiation.

Of the generalized species the only types having anything in common with *C. adersi* are the more robust *C. natalensis* and the considerably larger *C. leucogaster*. The latter has a fine silky coat like *C. adersi* and rather coarse throat hair but may not be far from the root of the smooth-necked radiation. The former is closely related to the *C. harveyi-nigrifrons* radiation. Both *C. leucogaster* and *C. natalensis* may have been dominant species in the past, one within the main forest block, the other over a wider area on the eastern side of the continent. A rare West African species, *C. ogilbyi* links *C. leucogaster* with *C. callipygus* and the other smooth-necked duikers. If the joining and separating of populations in the three main forest refuges is mimicked on a theoretical model it is possible to construct several permutations that would reproduce a size-graduated radiation of all the smooth-necked species and also accord with the real distribution patterns. For example, the proliferation of species can be illustrated by an imaginary projection (see diagram, top right on facing page) back through imaginary periods, one of forest fragmentation (dry) the other of connexion (wet).

The status of some species such as *C. rubidus* is still uncertain but there is the possibility that the Ruwenzori duiker is recapitulating the fate of other relic species that have been replaced by close relatives. If, as I suggest



- A *Cephalophus sylvicultor*
- B *Cephalophus spadix*
- C *Cephalophus callipygus weynsi*
- D *Cephalophus callipygus lestradei*
- E *Cephalophus nigrifrons kivuensis*
- F *Cephalophus nigrifrons hooki*
- G *Cephalophus harveyi*
- H *Cephalophus rubidus*
- I *Cephalophus leucogaster*
- J *Cephalophus natalensis*
- K *Cephalophus rufilatus*
- L *Cephalophus adersi*



in the profile of that species, *C. rubidus* is mixing with *C. nigrifrons kivuensis* along the lower boundaries of its alpine range, the resultant blurring of specific characteristics may illustrate one of the reasons for the close resemblance of some red duiker species, particularly in the structure of the skull.

Other evidence of hybridization concerns *C. harveyi* in central Kenya, where it is the common forest duiker up to about 3,000 m. On Mt Kenya, *C. harveyi* is replaced above this level by a very close relative, *C. nigrifrons hooki*, apparently without mixing, in spite of the latter's range being entirely encircled by Harvey's duiker. By contrast, there is evidence that *C. harveyi* crosses with a much less closely related but ecologically equivalent species, *C. callipygus*, on the Mau which is the narrow frontier of their contemporary ranges. Yet the latter species is sympatric with *C. nigrifrons nigrifrons* right across the main lowland forest block without hybridization. Two radically different species, *C. dorsalis* and *C. zebra* have been hybridized successfully in the Frankfurt Zoo.

These paradoxical contrasts emphasize the close genetic relationship of all duikers and illustrate the decisive part played by ecological adaptation when one population meets another. Thus *C. harveyi* and *C. callipygus* both occupy the main middle-sized forest duiker niche, whereas *C. nigrifrons* is very specifically adapted to swampy habitats.





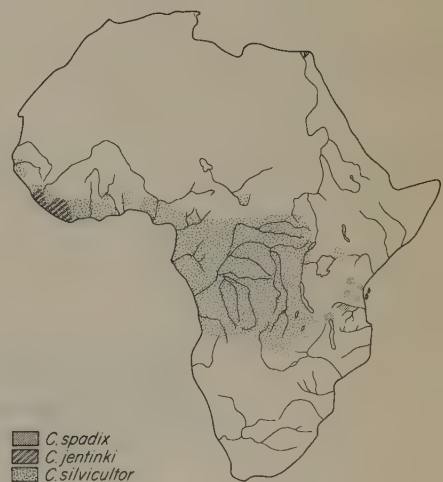
This situation has a fundamental significance for the nomenclature of duikers. Thomas (1903) first described a red duiker from the Mau by the name of *C. ignifer*. More specimens have been collected since and, as is generally the case with hybrids, there are characteristics of either parental stock or intergradations. In particular the length and texture of hair and the colouring are individually variable. St Leger (1936) noted that coats of the two adults skins available to her were thicker on the shoulders and harsher in texture than in *C. callipygus (weynsi)* but not as thick and harsh as in *C. harveyi*. Regarding these animals as a clinal link between the two populations, she treated them as races of a single species, a course that was later followed by Haltenorth (1963) and Ansell (1968). The clinal hypothesis was reinforced by the fact that populations of *C. callipygus* east of the Congo (Zaire) River lack a dorsal stripe and are smaller and brighter in colour, while the shoulders and throat are less thinly haired than in West Africa.

The smaller size and longer hair of *C. callipygus weynsi* in the Central Refuge might reflect a closer relationship with *C. ogilbyi*, while *C. c. callipygus* is a more advanced form. Alternatively, these apparently clinal differences could be the product of an advance in which a coarse-furred competitor has been displaced by the larger *C. callipygus* but the genotype of the latter has been altered through some hybridization. If this was so, the situation has an almost exact parallel in the three hyraxes, where a late invader from West Africa, *Dendrohyrax dorsalis*, has overrun *D. arboreus* north of Lake Victoria, in the process of which the two populations have hybridized (for details see Vol I, pp. 345—349), I have also described *C. callipygus* as one member of the fauna associated with the last eastward expansion of the lowland forest biome (Vol. I, pp. 69—74). Hybridization across the Rift Valley also occurs in the monkey *Cercopithecus mitis* and at precisely the same locality (see Vol. I, pp. 10—11, 235—240).

The giant yellow-backed duiker, *C. sylvicultor*, also reaches its eastern limit on the Mau and it is possible that the very similar *C. spadix*, which occupies isolated mountain forests within the range of *C. harveyi* is also a relic in retreat before its larger relative.

The approach offered here has been amplified in the profile of the Cephalophinae where the dietary and ecological implications of "main line" and peripheral habitats were outlined. The individual profiles also attempt to define the uniqueness of forms more exactly. However, duiker speciation has a still wider importance as an indication of the grand evolutionary drama enacted by all inhabitants of the African forests, a significance that is highlighted by the striking resemblances between some of the duiker's distribution patterns and those of *Cercopithecus* (Kingdon, 1980), *Colobus*, *Dendrohyrax* (Vol. I, pp. 149—153, 332—347), *Funisciurus* and the *Colomys-Malacomys* radiation (Vol. IIB, pp. 377—418, 572—575),

An accurate picture of the ecological and climatic vicissitudes of Africa will emerge when data from many other sources are collated. Eventually it may even be possible to suggest time scales for the climatic swings which undoubtedly governed the interaction of duiker populations. In the meantime I hope this tentative sketch will suggest productive lines of enquiry.





Blue Duiker
(*Cephalophus*
***monticola*)**

Family
Order
Local names

Ndimba (Kiswahili), Ntalaganya
(Luganda), Ikirungu (Lugisu), Nendi
(Lutoro, Lukonjo), Kasendi (Luragoli),
Shiseri (Kitereki), Kalili (Kisafwa),
Asesi (Kikinga), Akasasi (Kinyakyusa),
Kabanyet (Masai).

Bovidae
Artiodactyla

Measurements
head and body

60—65 cm

height

35—41 cm

tail

9—10 cm

weight

3.5—9 kg

horns

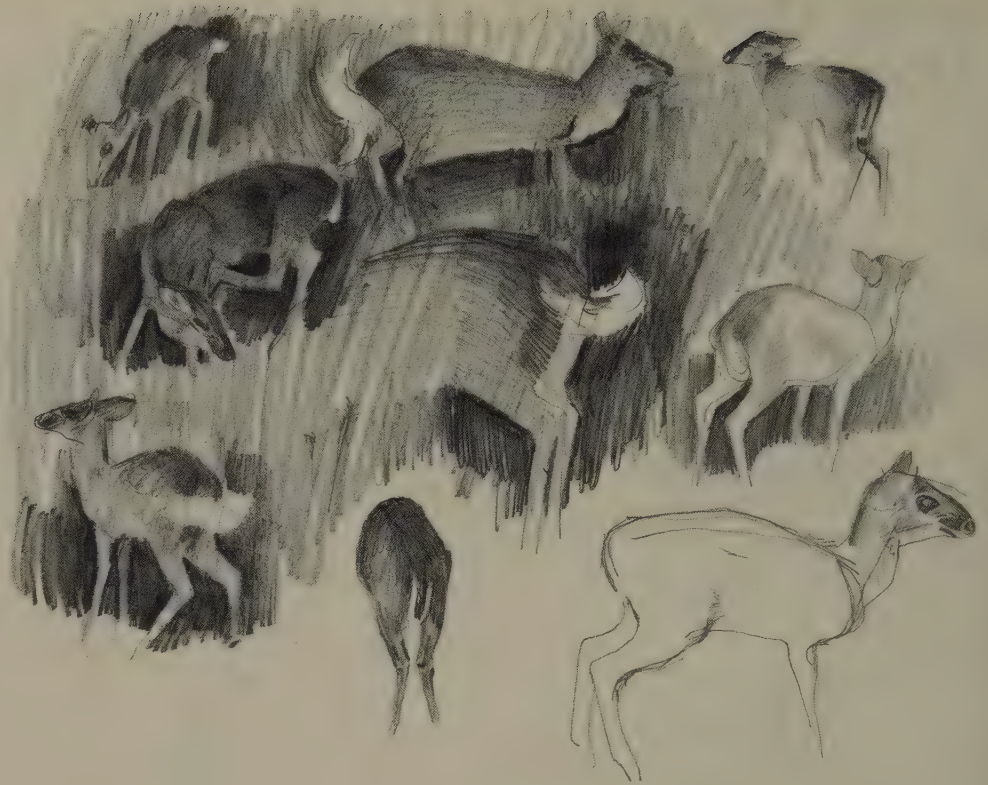
3—9 cm

Blue Duiker (*Cephalophus monticola*)

Races

<i>Cephalophus monticola</i> <i>aequatorialis</i>	Uganda, West Kenya and North-West Tanzania
<i>Cephalophus monticola</i> <i>lecki</i>	Eastern Coast and Mafia Island
<i>Cephalophus monticola</i> <i>schusteri</i>	Uluguru and Usambara Mountains
<i>Cephalophus monticola</i> <i>lugens</i>	Southern Highlands
<i>Cephalophus monticola</i> <i>sundevalli</i>	Zanzibar Island
<i>Cephalophus monticola</i> <i>pembae</i>	Pemba Island





This small dark-brownish grey duiker is the most widespread of all the duikers but also one that is subject to some considerable regional differentiation. Its coat colour shows some conformity with Glogers Rule, especially *C. lugens* and *C. pembrae* which occupy high rainfall areas.

Its presence on the island of Pemba, which has been separated from the mainland for a very long time by a deep channel, might be some indication of great age but is more likely to reflect this species' ability to swim—a blue duiker has been reported to have been seen swimming in the ocean off Natal. It also lives on Zanzibar, Mafia, and in West Africa, Fernando Po islands.

It also inhabits many ecological "islands" of forest all over the eastern part of the continent and can survive in quite narrow gallery forests as long as they are moist enough or if it has access to water. Its altitudinal range is also considerable and it has been recorded in montane forest on the Ruwenzoris and Elgon up to 3,000 m.

It lives under dense cover and is often one of the commoner animals in the undergrowth, where it feeds to a very large extent on fallen leaves and buds, often quite dry, and also on fruit, seeds and mushrooms. In Uganda commonly eaten leaves are those of *Milbraediodendron* and *Mammea africanaum*. It likes the seeds or fruit of *Maesopsis*, *Ricinodendron*, *Cordia*, *Musanga* and *Pycnanthus*, all common or even dominant trees of mixed and regenerating forests, has also been recorded as favouring fresh leaves of buckweed, *Isoglossa*, and *Brachylaena*, nettles, *Urtica* spp., as well as members of the *Ipomea* family and it enters forest-edge cultivation to nibble sweet potato tops. Grimm (1970) noted a large quantity of ants belonging

to the solitary species *Palthothyreus tarsatus* in one stomach; which must have been picked up one by one. In a quantification of the composition of stomach contents Gautier-Hion *et al.* (1980) recorded 78.5% fruit, 20.3% leaves and very small quantities of animal matter, flowers, and gum.

Blue duiker generally forage on the forest floor, only emerging into glades or along the forest edge at dawn or dusk, its most active feeding periods. Vaughan Kirby 1899 saw several in a tree some four metres above the ground; although several duiker species have been seen clambering into trees, this must be very unusual behaviour on any account.

Visually the most striking characteristic of this duiker is the continuous flickering of the tail. The fringing white hairs are slightly crinkled and reflect light very well, so that the exposure of the hairs often looks like a small flash-light going off and on along the dark forest floor. This heliographic signalling device is somewhat similar to that of the South American forest rodent, *Myoprocta*.

Like the other duikers it has a hesitant high-stepping gait, is sharp-eyed and has a good sense of smell. It also makes a loud sneezing whistle when running away. It is said to make a cat-like yowl and will bleat when in distress. Mutual grooming is very common in captives with the greatest attention centred on the top of the head. This area is marked by a hair whorl on the young and meetings between adults that are familiar with one another may be accompanied by grooming of the frontal tuft and mutual face rubbing.

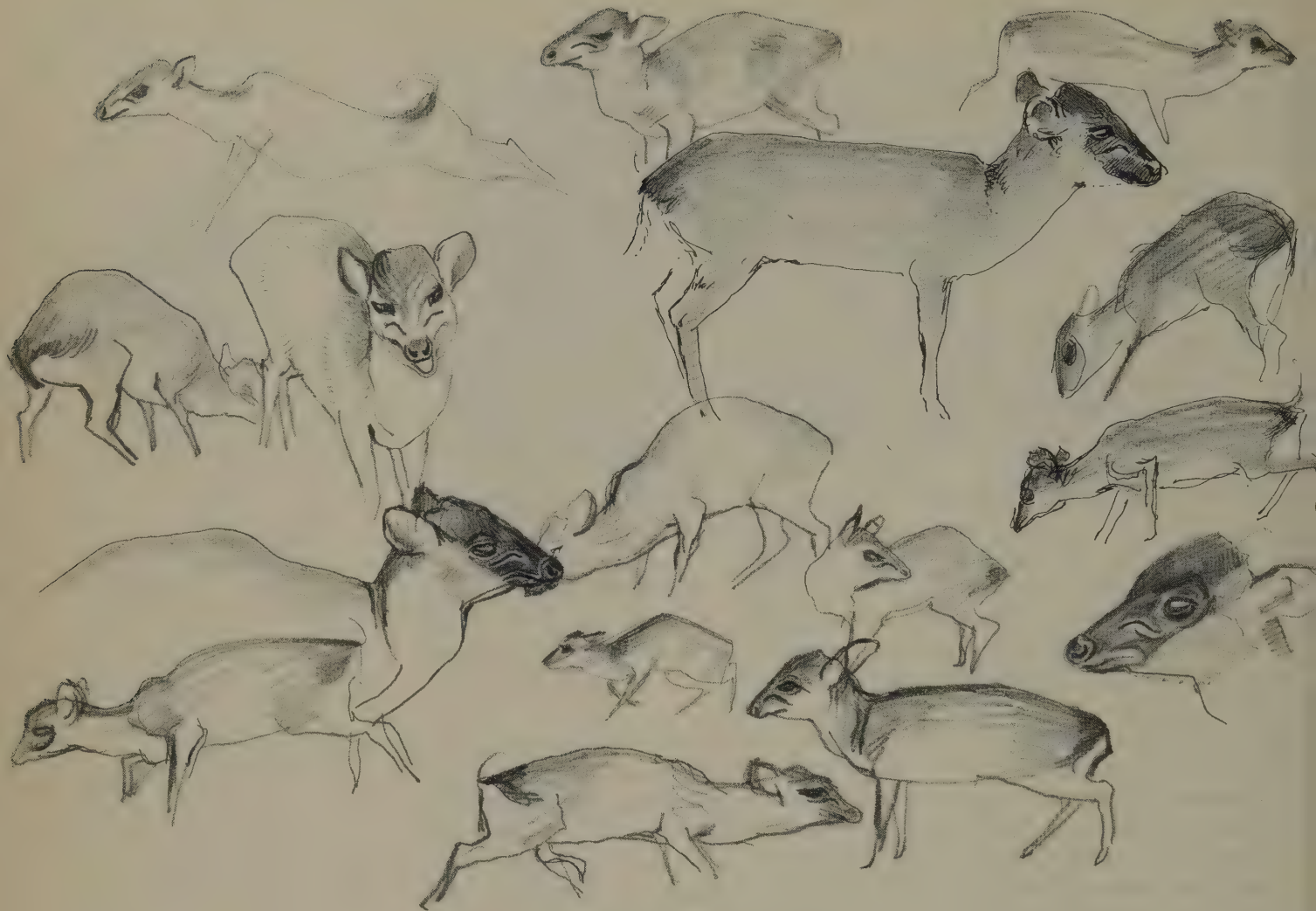
The West African *C. maxwelli*, which may actually represent the same species and is certainly the allopatric ecological equivalent, has been studied in captivity by Aeschlimann (1963) and Ralls (1974). They noted that even when more females were available a male formed a close bond with only one. When Ralls introduced strange duiker into a pen the incidence of head-rubbing within the established group increased, and she found that marking of the territory's perimeter by the male generally preceded feeding and resting.

Most movements and feeding occur during the evening and early morning, but short activity periods tend to be alternated with rest and rumination throughout the day and perhaps the night. I seldom came across blue duiker at night but I did collect one after midnight which proved to have a congenital malformation of the lower incisors, which must have hampered feeding. It was thin and stunted although adult. Verheyen (1951) noted seeing blue duiker in the relatively dry Upemba Park, crossing open country to reach water and staying near water during the heat of the day.

In this locality, Vincke (1950) recorded a parasite resembling the malarial *Plasmodium* in the blood of *C. monticola*, the mosquito vector of which proved to be *Anopheles concolor*. When irritated by flies blue duiker have been seen to snap at them.

An observer in the forest is probably seen by many more blue duiker than he himself sees, because they tend to freeze at the slightest alarm and only run away sneezing if encountered unexpectedly at close quarters. The golden cat, serval, leopard, crowned hawk eagle and snakes are probably the most important predators of this species. Jackson (1956) found a fawn inside a large mamba and pythons are known to eat them.





This species is easily netted and snared because of its localized habits and pathways. Males can be called up by experienced hunters who imitate the sneezing, which suggests that this call might be of greater significance as an auditory advertisement than an alarm call.

The possession of horns by the male only, his greater activity in maintaining contact with the female, marking the territory and fighting other males suggests that sexual roles are more highly differentiated in this species than in some other forest duikers.

Recruitment in this duiker is probably fairly high as lactating females with young at heel are sometimes pregnant as well. Ketelhodt (1973) has shown that there are scattered births throughout the year in South Africa but a marked peak in the rainy season, September—November. I have several birth records for Uganda and western Kenya in January and February, which is, instead, a dry period. Smithers (1966) records births in the dry months of June, August and October in Zambia but Loveridge notes a female from Rungwe lactating in April.

The male identifies oestrus through the usual urine testing and courtship is marked by the pair circling round one another in excitement. The female

raises her tail shortly before the male mounts and copulation is preceded by much mutual rubbing of both sides of the face.

Gestation has been reported at 167 days (Brand, 1963). At birth the single young is about one tenth of the mother's weight. It is precocious and able to run within half an hour, although it usually remains well hidden and only emerges for a suck and brief contact with the mother, which stimulates excretion by licking the anal region. Aeschlimann noted that lactating *C. maxwelli* drink regularly and the young put on 50 g per day. They start to browse at two weeks and are thereafter weaned gradually. The male's horns first appear at two-and-a-half months but both sexes appear to be sexually mature only at about three years of age. Captives have been known to live ten years.

The pelts of *C. monticola* were greatly favoured for the making of karosses in Uganda and also in Rungwe district. I have found karosses which contained 60 skins offered for sale in tourist hotels.

Since this profile was written, Dubost (1980) has published a study of their ecology and social life in Gabon. By radiotracking 15 individuals and catching many others he discovered that pairs jointly occupy exclusive permanent territories of 2.5–4 ha with an overall density of 70 individuals per sq. km and an annual turnover of 7–10%.

Dubost considered that the habits of this species of duiker resemble those of many savanna species and he remarked especially on a preference for relatively open undergrowth which facilitates visual communication as well as movement. He considered that this small herbivore improves its chances of escaping predators by being strictly diurnal and living in pairs or small temporary families.

The blue duiker is very unusual in that each animal follows its own rhythm of activity and these appear to be highly idiosyncratic. This may be linked with exceptional activity. Adults daily traverse almost their entire territory and the members of a family have no difficulty in maintaining frequent contacts. Yet, once the young are mature, they invariably leave the parental territory entirely and never maintain any sort of link with either parent. Males and females mark out their home range continuously by means of urine, dung, facial secretions and bark-bruising with the horns. The latter is frequent wherever the vegetation is suited to easy horning and is mostly found on the periphery of the territory where adults of both sexes spend 25–33% of their time. Core areas tend to centre on relatively open undergrowth. Animals rarely chose dense cover to rest in (16% of all records) and preferred the foot of a tree (44%) or open areas (40%). Rain was an important consideration in the choice of a resting site. The exceptionally intensive use of a small territory without any overlap or contact between neighbours, peculiar activity patterns and expulsion of adult young all suggest that *C. monticola* has developed an unusually tight fit between population density and food resources.



**Ader's Duiker,
Dwarf Red
Duiker
(*Cephalophus
adersi*)**

Family

Bovidae

Order

Artiodactyla

Local names

Nunga (Kiswahili), Kungu marara
(Kipokomo).

**Measurements
head and body**

66—72 cm

height

30—32 cm

tail

9—12 cm

ear

7—8.3 cm

weight

6.5—12 kg

horns

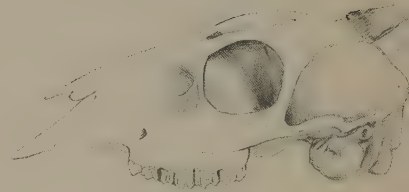
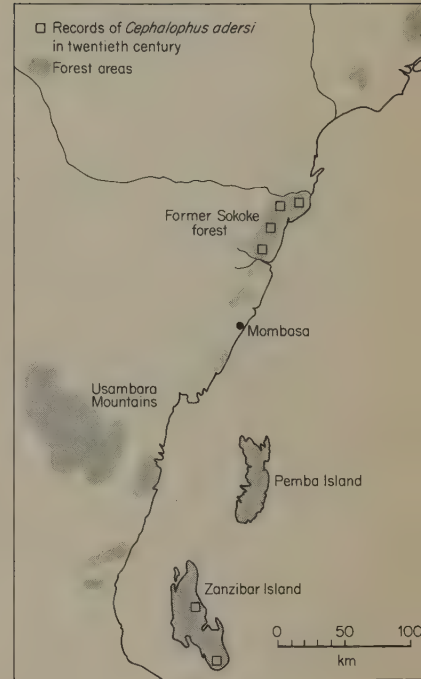
3—6 cm

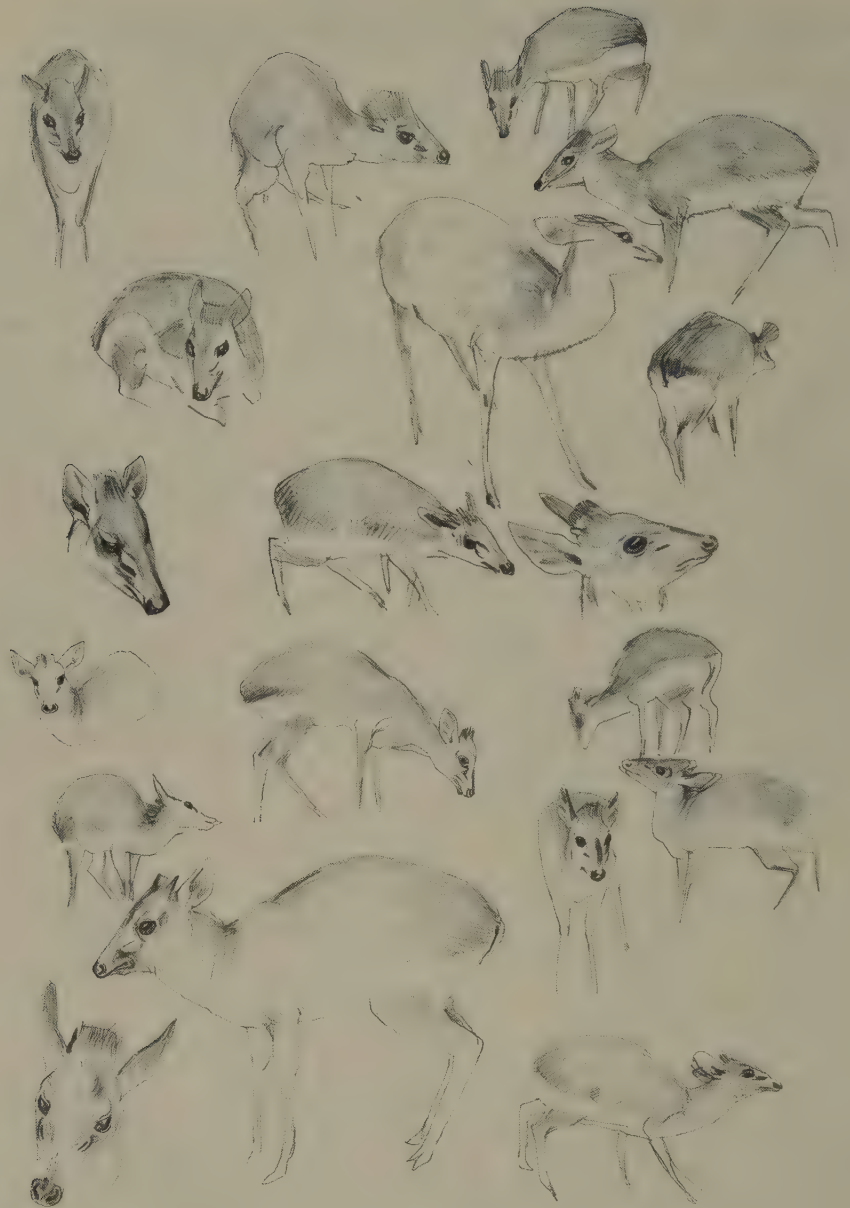
Ader's Duiker, Dwarf Red Duiker (*Cephalophus adersi*)

This duiker is unmistakable because of the white band across its buttocks and the white freckling on its legs. The ground colour is a washed-out tawny red becoming somewhat greyer on the neck; the crest is red and there is a black and white spot just above the hooves. The fur is particularly soft and silky.

Hunters on Zanzibar have reported that these duikers consistently average about 12 kg at Kiwengwa, in the mideastern part of the island, whereas they are paler and only about 7.5 kg in the Jozani forest in the extreme south (Darwish, personal communication).

These duikers are also widespread in the forests, woodlands and thickets north of Mombasa, almost up to the Somali border. They often live in quite dry scrub near the sea or among coral outcrops and can manage without water. They are diurnal and apparently lie very close at night for, over several years of hunting, Darwish (personal communication) never saw them by torchlight, even after quartering country where they had been seen regularly during the day.





This species coexists with *C. natalensis harveyi* on the mainland and with *C. monticola sundevalli* on Zanzibar. It seems to be able to live under drier conditions than either of these species but no comparison of their behaviour or ecological separation has been attempted.

This species has been kept successfully in captivity, where they breed more or less continuously within small pens. As the habitat of this species is shrinking rapidly and they are hunted vigorously, it should be a worthwhile enterprise to breed them in parks or zoos.

White-bellied Duiker (*Cephalophus leucogaster*)

Measurements head and body

78—95 cm

height

51 cm

tail

8—13 cm

ear

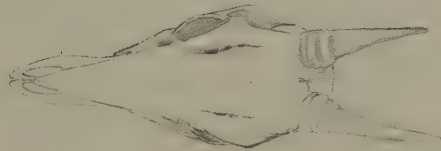
5—8 cm

weight

18 kg

horns

5—10 cm



This is one of the palest of the forest duikers, with warm sandy brown forequarters graduating towards grey near the black dorsal line. Near the rump there is a warmer flush of rufous and the crest is rich orange while the front of the face is black, as are the heels and hocks, which contrast strongly with the white belly and inside of the legs. Immediately behind the ears, the nape of the neck fur is short but the rest of the neck is covered in long coarse hair. The tail has a fluffy black and white tip.

Earlier I suggested that this may be the somewhat specialized remnant of a formerly dominant type. The skull is deeper and more robustly built than that of most of the coarse-necked duikers. The rather flat nasals also form a less tapered nasal tube.

The teeth are relatively robust and the angle of the lower jaw has a flange which, instead of facing backwards as in the other coarse-necked duikers, tends downwards, so that the masseter has a more vertical action. The digastric muscle might also be relatively larger, implying a wider gape and a stronger bite.

Rahm (1966) collected one specimen with *Klainedoxa* fruits in the stomach. As these are relatively large and very hard fruits, this isolated observation is consistent with the specialization in tougher foods that is implied by the jaws and teeth. Gautier Hion *et al.* (1980) recorded 73% fruit, 25% leaves and 2% flowers in stomach contents from Gabon.

Dorst and Dandelot (1970) describe its habitat as dense forest and particularly secondary growth. The species is predominantly diurnal.

This species has been recorded from various localities within the Central Forest Refuge between the Congo River and Uelle. Blancou (1958a) described this species as plentiful in Gabon and Congo Brazzaville.

This species was thought to exist at one time in the Kayonza forest and it is tentatively included in the East African faunal list; it might also occur in Bwamba. Details of the natural history of this species would be most interesting as no information at all is available to date.



**Red-flanked
Duiker**
(*Cephalophus
rufilatus*)

Family
Order
Local names
Tili (Madi)

Bovidae
Artiodactyla

**Measurements
head and body**

75—80 cm

height

35—38 cm

tail

8—9 cm

ear

7 cm

weight

12—14 kg

horns

5—9 cm

Red-flanked Duiker (*Cephalophus rufilatus*)

Race

Cephalophus rufilatus rubidior

This is a prettily coloured duiker, bright orange-red on the neck and body with bluish grey gauntlets on the limbs and a grey back which is darker in the eastern race than in the western. The black nose and lower lip contrast strongly with the white jaws and upper lip and the ears also have black and white flashes. The frontal is variably streaked with black and there is a prominent vertical tuft of black hair. The profile of the nose is straight and the skull is narrow. Relative to the size of its head this species has the largest and deepest preorbital gland pits of any red duiker. This presumably signifies exceptionally active marking behaviour.

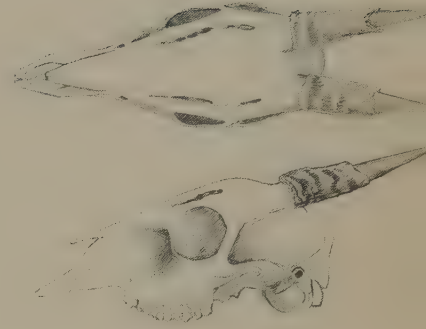
This species ranges along the northern margins of the forest block as far as the Albert Nile. It was once widely distributed in the West Nile district.

When forest is in retreat a variety of vegetation types takes its place. Among them are elephant grass, *Pennisetum purpureum*, and dense growths of shrubs such as *Capparis*, *Teclea*, *Toddalia* and *Acanthus arboreus* with a few persistent trees such as *Sapium* and *Diospyros*. These are the favoured habitats of this species and because thick vegetation follows along drainage lines, this duiker is often found there very far from true forest.

Ansell (1968) remarked that, being a forest edge species, *C. rufilatus* would probably be favoured by the destruction of high forest and doubtless withstand considerable hunting pressure as long as enough suitable habitat remained available. The last factor is crucial and there have been no recent reports on this species' status in the very highly populated West Nile district.

Happold (1973) described the red-flanked duikers as crepuscular, commonly seen feeding in the open or in glades, singly or in pairs, but bouncing for cover with head down if disturbed. They make a shrill bark. The single young is said to be born during the dry season.

In his study of the Cephalophinae, Heyden (1963) placed this duiker together with *C. nigrifrons* within a superspecies. Although it belongs to the same coarse-haired group this is nonetheless a quite distinct species.



Ruwenzori Red Duiker (*Cephalophus rubidus*)

This duiker has a glossy rufous coat with long coarse hair on the neck changing to dense soft fur over the hindquarters. The belly is white. The hindlegs are almost black and there are dark brown markings on the joints of the forelegs. There is a black or dark brown blaze on the forehead. Down the midline of the back and neck there is a zone of dark grey underlying the uniform red tips of the fur while the underfur of the flanks is cream. This peculiar arrangement is only shared by *C. rufilatus*, which makes it unlikely that *C. rubidus* is a race of *C. nigrifrons* and suggests that some distant affinity with *C. rufilatus* is possible in spite of a considerable difference in size.

Schwartz (1914) treated this as a race of *C. natalensis* and St Leger (1936) regarded it as a high altitude race of *C. nigrifrons* but she correctly pointed out that *C. n. kivuensis* occurs on the lower slopes of the Ruwenzori Mountains and that this race was commonly confused with *rubidus* in spite of the former having a thinner harsher coat and a grizzle.

The Ruwenzori duiker is an inhabitant of the alpine and subalpine zones and I have seen it feeding close to the snowline. Its lower limits probably coincide with the bamboo zone but I suspect that *C. rubidus* and *C. n. kivuensis* tend to hybridize where their ranges overlap. I collected a form, possibly an intermediate one, at about 3,000 m in 1960 and the British Museum Ruwenzori expedition collected two duikers at a similar altitude which exhibit somewhat redder, less grizzled and thicker coats than typical *C. n. kivuensis*. It is possible that a similar situation occurs also in a small area of North Kigezi, where bright russet duikers have been seen at 2,200 m.

Ruwenzori Red Duiker (*Cephalophus rubidus*)

Family
Order
Local names
Isuku (Lukonjo)

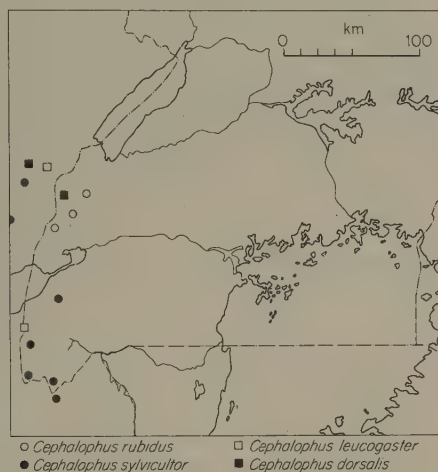
Bovidae
Artiodactyla

Measurements head and body

75 cm
height
45 cm
tail
10 cm
weight
15 kg
horns
8—9 cm
skull
15.3—16.5

Because of variation in the length of the maxilla and premaxilla the skull measurements are a poor guide to relative size in red duikers but a small series of *C. rubidus* averages 1.5 cm less than *C. n. kivuensis* skulls.

The Ruwenzori duiker often feeds in the open on exposed and rocky scree as well as in boggy, densely overgrown or wooded areas, (see Vol. I, pp. 25—27, for a description of its habitat). It is both diurnal and nocturnal, but its activity patterns may vary seasonally. Where it is abundant it is snared by Bakonjo hunters, who carry smoked meat back to the villages 2,000 m below, leaving gifts of eggs in wayside shrines to placate the spirit of the mountain.





**Natal
Red Duiker**
(*Cephalophus
natalensis*)

Family

Bovidae

Order

Artiodactyla

Local names

Funo, Ngarombwi (Kiswahili).

Measurements
head and body

75—87 cm

height

40—43 cm

tail

9—14 cm

ear

6.5—8.7 cm

weight

12—14 kg

horns

6—10 cm

Natal Red Duiker (*Cephalophus natalensis*)

This is one of the smaller red duikers and is without very distinctive features. The body and legs are red, the throat is pale and the chin is white. Immediately above the hooves and on the nape of the neck the fur is grey. The tuft between the ears is black and red.

The animal's relatively small size and slightly less harsh fur combine with its distribution to suggest that *C. natalensis* is an older form of the same lineage as *C. harveyi* and *C. rufilatus*. Forest fauna from the extreme south-east of Africa can generally be taken to have had a long disconnection from the tropical forest belt (see Vol. I).

C. natalensis suffers no competition from any other large duiker and its habits appear to be typical of the genus as a whole. Commonest on the coastal strip, it also ranges through a variety of riverine vegetation types as well as montane forest.

Its feeding is opportunistic and captives will take meat readily. *C. natalensis* has been seen to roll the hard-shelled monkey orange until it lies against a tussock or root and then ram the shell open with the horns to get at the pulpy seeds, which are sucked and spat out. This species is diurnal.

Heinichen (1972) published some observations on *C. natalensis* in South Africa and most of the generalizations made in the duiker profile hold true for this species. It has been observed to make the most prodigious leaps during capture operations in southern Africa.





**Harvey's Red
Duiker
(*Cephalophus
harveyi*)**

Family

Bovidae

Order

Artiodactyla

Local names

Funo (Kiswahili), Esero kumei (Masai),
Nguni, Ndunia (Kikuyu), Pepeechi
(Kiliangulu).

Kinambure (Kimachame)

Measurements

head and body

85—95 cm

height

44.5—50 cm

tail

11—15 cm

ear

6—8 cm

weight

13—16 kg

horns

6—12 cm

Harvey's Red Duiker (*Cephalophus harveyi*)



In East Africa this is the most widespread of the red duikers. It has a rich red colour on the rump and back becoming lighter below. The bridge of the nose and centre of the crest are black. This line is continued down the back of the neck, where it gives way to a dark freckle and in the southern parts of its range this melanic tendency extends as far as the shoulders. In this area, the legs are also entirely a dark sepia brown. By contrast, animals from Mt Kenya, where they are sympatric with the darkly freckled *C. nigrifrons hooki*, show minimal areas of dark colour.

In spite of being related allopatric species and in spite of intermediate animals being known from the areas where their ranges meet, I prefer to maintain *C. harveyi* and *C. natalensis* as distinct species.



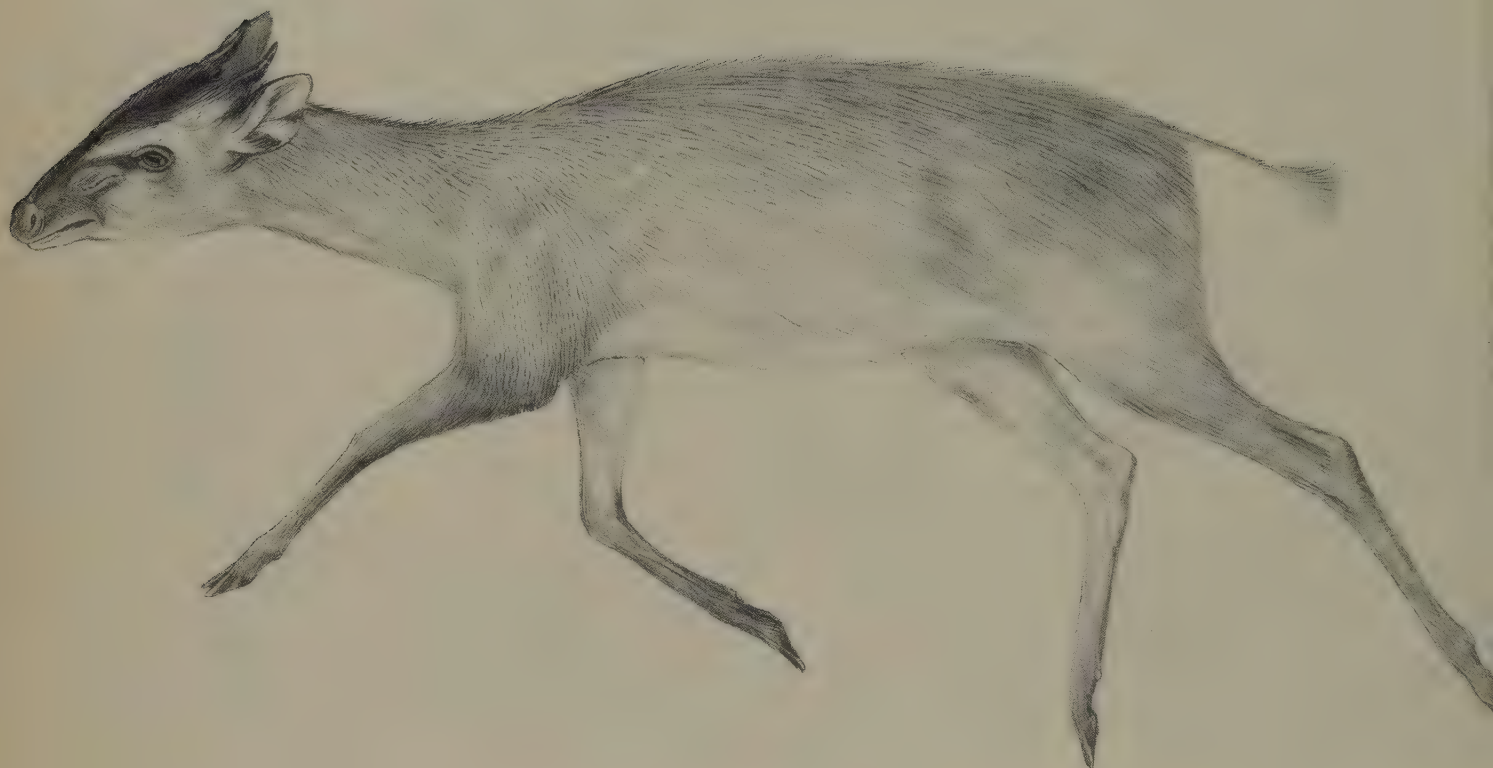
The principal reason for this is that I consider *C. harveyi* could be equally closely related to *C. nigrifrons*, *C. rubidus* and perhaps *C. rufilatus*. I have not had the opportunity to measure or make very detailed comparison between the generalized proportions of *C. harveyi* and the long-limbed swamp-adapted *C. nigrifrons* but there is much to suggest a common ancestry, and the possibility of a complex relationship would be lost to view if the species was lumped with *C. natalensis*.

The proliferation of duiker, guenon, squirrel and other rodent species in the main forest block represents each group's response to the diverse food supplies and variety of microhabitats and niches in that rich and complex environment. Intense competition has eliminated all but the most advanced or specialized so that we have little indication of the course or rate at which such evolutionary radiations have taken place. Eastern isolates such as Harvey's duiker and the Natal red duiker may provide important information about the evolutionary process if their relationship to other duikers is more accurately defined and this is a task that remains undone.

It has already been stressed that a major mechanism assisting speciation in forest mammals has been the oscillating climate of the Plio-Pleistocene, which has allowed several excursions of forest flora and fauna to reach across to the Indian Ocean. The animal and plant species stranded in the degraded or minuscule forests of the eastern littoral have had various fortunes, but one can assume that most have adapted to local conditions and their status as "endemics" often stems from that adaptation. Types such as the mitis monkey (Vol. I, p. 235) and Tanganyika mountain squirrel (Vol. IIB, p. 393) have subspeciated very extensively in response to local isolation and *C. harveyi* also shows some localized differences in colouring which might, on further study, justify the recognition of subspecies. It is however more important to recognize that the forces of selection on a single (or very limited number) of representative species, in small, impoverished and discontinuous patches of habitat are fundamentally different to those exerted on populations of the same animal within a large community of congeners in the main forest block. (For the guenons, this situation is discussed in some detail in Kingdon, 1980.) On the face of it, *C. harveyi* can be held to typify the generalized, conservative type from which *C. nigrifrons* evolved, but a detailed comparison of these and other duikers is needed to determine whether this is so or whether Harvey's duiker shares any of the specialized traits of its swamp-loving relative. Any evidence for regression (notably in limb proportions) could imply that incipient specializations could be reversible outside the range of competitive, multi-species duiker communities.



Much remains to be learnt of the ecology of this species in different areas of its range, especially on Mount Kenya. Such studies need to be closely integrated with a more detailed knowledge of duiker anatomy and physiology. Considering the rarity of duikers and especially of *C. harveyi* in museum collections it is important that naturalists and wildlife departments should make efforts to preserve and document skins, skulls and especially the skeletons of these still quite abundant and widespread animals.



**Black-fronted
Duiker**
**(*Cephalophus*
nigrifrons)**

Family

Bovidae

Order

Artiodactyla

Local names

Kichachu (Kikuyu), Efumbiri (Rukiga),
Sikwet (Sebei).

Measurements
head and body

80—104 cm

height

48—51 cm

tail

7.5—11.5 cm

ear

6.5—9.7 cm

weight

17—18 kg

horns

7—12 cm

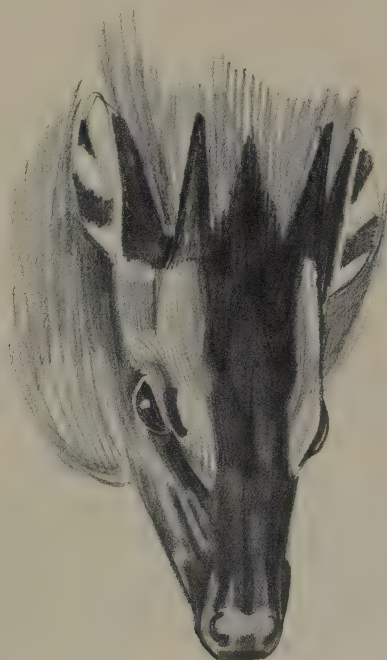
Black-fronted Duiker (*Cephalophus nigrifrons*)

Races

<i>Cephalophus nigrifrons kivuensis</i>	Bufumbira and Ruwenzori forests
<i>Cephalophus nigrifrons fosteri</i>	Mt Elgon 2,400—3,500 m
<i>Cephalophus nigrifrons hooki</i>	Mt Kenya

This relatively long-legged and coarse-haired red duiker is essentially a montane or high altitude species in East Africa but it occurs throughout the Congo basin in swamp forest. The lowland forest form, *C. n. nigrifrons* resembles *C. harveyi* and is very closely related. *C. n. kivuensis* has an exceptionally glossy coat, extensive black grizzling on the back and very dark legs. *C. n. fosteri* and *C. n. hooki* clearly derive from this stock but the former is smaller and very much redder on the head and throat. *C. n. hooki* is duller all over, as though lightly dusted with chalk, and it has longer and softer fur. Bouillon and Leleup (1954) noted that some specimens of *C. n. kivuensis* are without inguinal glands (a characteristic that was once used by taxonomists to separate the glandless blue duiker, *C. monticola*, from the other *Cephalophus* species).

Rahm and Christiansen (1963) first noted that *C. n. kivuensis* used regular pathways each day to visit swamps. This is particularly conspicuous during the dry season, as they may go far out into the valley swamps during





Cephalophus nigrifrons kivuensis.

the day to feed on sprouting vegetation and then return up the mountain sides to shelter for the night in dense tangles. Around the Bwindi swamp this habit is well known to the local trappers, who snare the duiker on their pathways, particularly during the drier months of June—July and January—February.

They feed on a wide variety of fruits and succulent vegetation, including balsam, *Impatiens*, wild coffee and other Rubiaceae. They are not, however, a pest to cultivation, scarcely ever entering gardens or fields. In Gabon, Gautier-Hion *et al.* (1980) recorded 71.6% fruit and 27.7% leaves in their diet.

Like the other duikers they have territories, marked out with the facial glands and a loud whistle-like call. They also make a loud thumping sound. Foster was assured by the Sebei that the animals made the noise in their chests. If this is so, it raises the interesting possibility that this species, dwelling on soft ground, mimicks the duiker foot-stamp with a vocal equivalent.

The Elgon race inhabits all habitats between 2,400 and 3,500 m but is commonest at 3,000 m, "where it breeds in the thickest parts of the bamboo forest where the old dry bamboo leaves lie so thick on the ground that they advertise the approach of even the smallest carnivorous animal long before it can reach the doe and young." (Foster in St Leger, 1934). On Mt Kenya, likewise, they are commonest in the bamboo on the south-west face between 2,600 and 3,000 m.

These duikers are subject to very heavy hunting but pressure is most severe on Mt Elgon.



Peter's Duiker
(Cephalophus
callipygus)

Family

Bovidae

Order

Artiodactyla

Local names

Esea (Kidorobo), Minde (Nandi), Ensuku
((Luganda and Lunyoro), Ngajulu
(Lusoga), Enuma, Enchuru (Runyankole),
Kamosere (Sebei).

Measurements
head and body

100—101 cm

height
56 cm

tail
8—10 cm

ear
9.5—10 cm

weight
16—20.5 kg

horns
7—13 cm

Peter's Duiker (*Cephalophus callipygus*)

Races*

<i>Cephalophus callipygus weynsi</i>	Uganda west of Victoria Nile
<i>Cephalophus callipygus barbertoni</i>	East Uganda and West Kenya
<i>Cephalophus callipygus lestradei</i>	Possibly along eastern shore of Lake Tanganyika

This rather large duiker is generally duller in colour and has a much softer finer coat than the other red duikers found in East Africa. The race found in the Central Refuge, *C. c. weynsi*, is sometimes treated as a species because it lacks a dorsal stripe and has slightly longer fur on the neck than typical *C. callipygus* in the Cameroon Gabon Refuge. The legs of *C. callipygus* are darker than the body and *C. weynsi* is rather variable in the extent of dark brown on its shoulders and back. This trait is taken to an extreme in *C. c. lestradei*, some specimens of which are almost entirely dark brown (Groves and Grubb, 1974). These large duikers were collected in Burundi and similar animals have been sighted in the Gombe Stream National Park and in the Mahali Mountains. While it is possible that *C. spadix* occurs in these Tanzanian localities, it now seems more likely that the animals are *C. callipygus lestradei*.

The expansion of forest and forest fauna from the Central Refuge across the northern shores of Lake Victoria is thought to have been a relatively recent development (Hamilton, 1975). The intrusion of typical lowland rain-forest species along this northern route was discussed in Vol. I and this duiker is representative of that fauna.

This is a diurnal species belonging to true forest not found in the outlying riverine strips and galleries. Nonetheless, it may flourish in logged areas within the forest benefitting from the dense growth at low levels. This species and bushbuck are the dominant bovids in many Uganda forests.

I have watched *C. callipygus* picking up large quantities of *Spathodea* flowers off the forest floor and stomachs have contained mushrooms as well as fruit and shoots. Gautier-Hion *et al.* (1980) recorded 83% fruit and only 16% leaves (1% flowers) which suggests that this is the most completely frugivorous of all the duikers.

Although skilled at avoiding contact with intruders, deliberately running up to a tree trunk or bush to peer out at an approaching person or animal from cover, they are vulnerable to snares set in their regularly used pathways and so are commonly harvested forest animals. They are also readily netted but are capable of breaking through the beaters. When captured as adults, they are difficult to keep alive and are extremely nervous and liable to damage themselves.

I have found hair from this species in the dung of leopards, and Sugiyama (personal communication) saw one being pursued by a golden cat.

* *C. ignifer* (Thomas, 1903) from the Mau, Kenya probably a hybrid between this species and *C. harveyi*.





Abbot's Duiker
(*Cephalophus*
***spadix*)**

Family

Bovidae

Order

Artiodactyla

Local names

Minde (Kiswahili), Mende (Kichagga).

Measurements
head and body

97—140 cm

height

66—74 cm

tail

13 cm

ear

10 cm

weight

52—60 kg

horns

8—10 cm

Abbot's Duiker (*Cephalophus spadix*)

This large, very dark brown duiker is evidently closely related to *C. sylvicultor* and probably represents the relic of an ancestral population. Its distribution in the isolated montane forests of Tanzania has probably protected it from replacement by its larger and more highly evolved descendant.

A hint of the yellow back of *C. sylvicultor* is visible in the form of a small grey patch above the root of the tail. It has a red crest and there is a strong red suffusion on the belly and inside of the legs.

In spite of intensive hunting, it is still fairly common on Kilimanjaro between 1,300 and 2,700 m in forest and high altitude swamps.

Ionides (1965) remarked on its use of diagonal pathways along the side of hills. This is primarily a nocturnal species which lies up during the day in the dense forest undergrowth or among bracken. Because of its use of regular pathways it is easily snared and dogs are used to bait it. It has been known to kill dogs when cornered, at which time it gets its back against a tree or it may take to water (T.G.R., 1949).

The species is thought to be mainly frugivorous; in September they have been recorded feeding on the leaves of a balsam, *Impatiens elegantissima*, (at this time no trace of young could be found).

They occur near Lake Manyara, on Mt Rungwe, in the Usambaras, the Ulugurus and Uzungwa mountains, localities in which they are now very rare because of the destruction of their habitat. Very dark duiker have been seen in the Gombe Stream National Park and in the Mahali Mountains, and Schouteden (1945) allocated some dark duiker from Ruanda to *C. spadix*, (as was indicated in the map on p. 70, Vol. I). Later, Groves and Grubb (1974) found that these animals are in fact a melanic race of *C. weynsi* type. It is possible that the dark duiker east of Lake Tanganyika also belong to this group and not to *C. spadix*.





**Yellow-backed
Duiker**
(*Cephalophus
sylvicultor*)

Family

Bovidae

Order

Artiodactyla

Local names

Kipoke (Kiswahili), Enkanda (Rukiga),
Mbolet (Kipsigi), Enzororo (Runyankole),
Kamasaret (Sebei).

Measurements
head and body

150—190 cm

height

70—87 cm

tail

18—20 cm

ear

11.5 cm

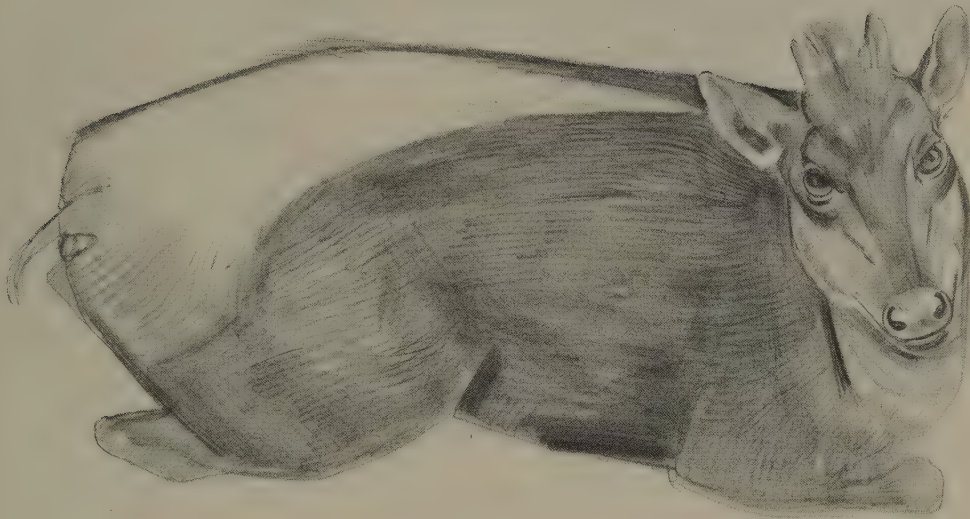
weight

45—80 kg

horns

11—21 cm

Yellow-backed Duiker (*Cephalophus sylvicultor*)



This is the largest of the duikers, with a slightly bovine look to its broad-nosed face. It is dark greyish brown and the yellowish-white back is a vivid feature, although it is not nearly as conspicuous in the field as one might suppose, for the hair lies close if it is skulking and becomes no more than a pale streak. Its proper role is undoubtedly social and the hair can be erected in display, although erection of this patch has only been recorded in captivity under conditions of stress. It has been suggested that the yellow patch might have a territorial display function or cover a glandular area, but I have found no deposit on the hair nor has skinning revealed obvious glands.

This species ranges across the whole of the tropical African forest block to western Uganda, with populations on Elgon and on the Mau in Kenya. In Zambia and Angola it occupies rather drier habitats but it is in general a true forest species and in East Africa is almost entirely an inhabitant of montane forest. However, throughout its range it is very locally distributed in pockets of suitable habitat, where it is apparently quite numerous. In Bwindi Forest Reserve, the selective but widespread felling of trees by pit sawyers has opened up the canopy and encouraged undergrowth; where this forms a tangled canopy two or three metres above the ground there is sporadic evidence of the duiker's presence, as there is throughout the reserve, but in certain semi-shaded valleys (where tree ferns, *Cyathea*, are often numerous),



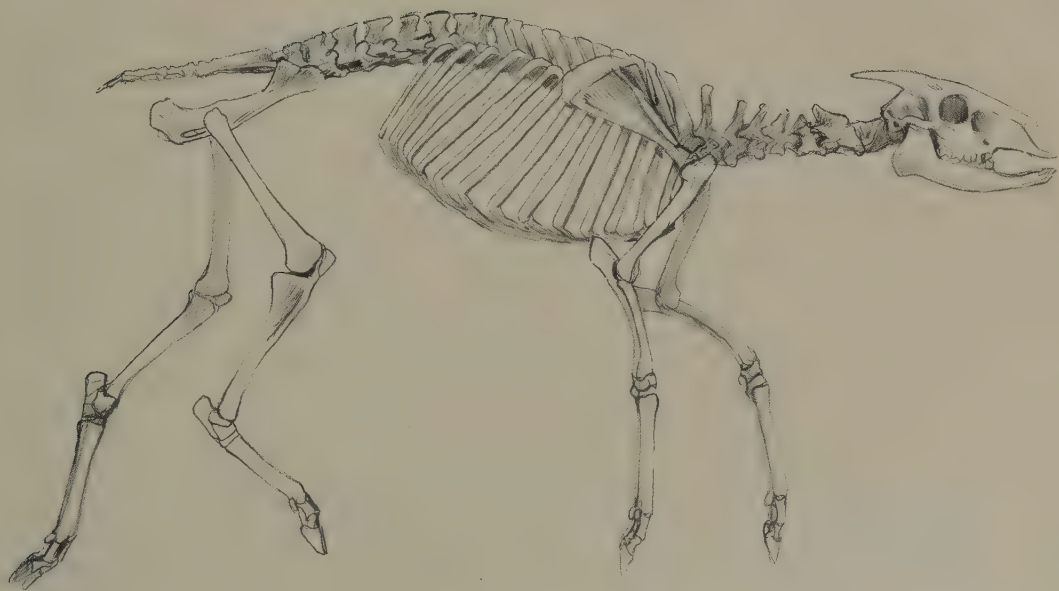
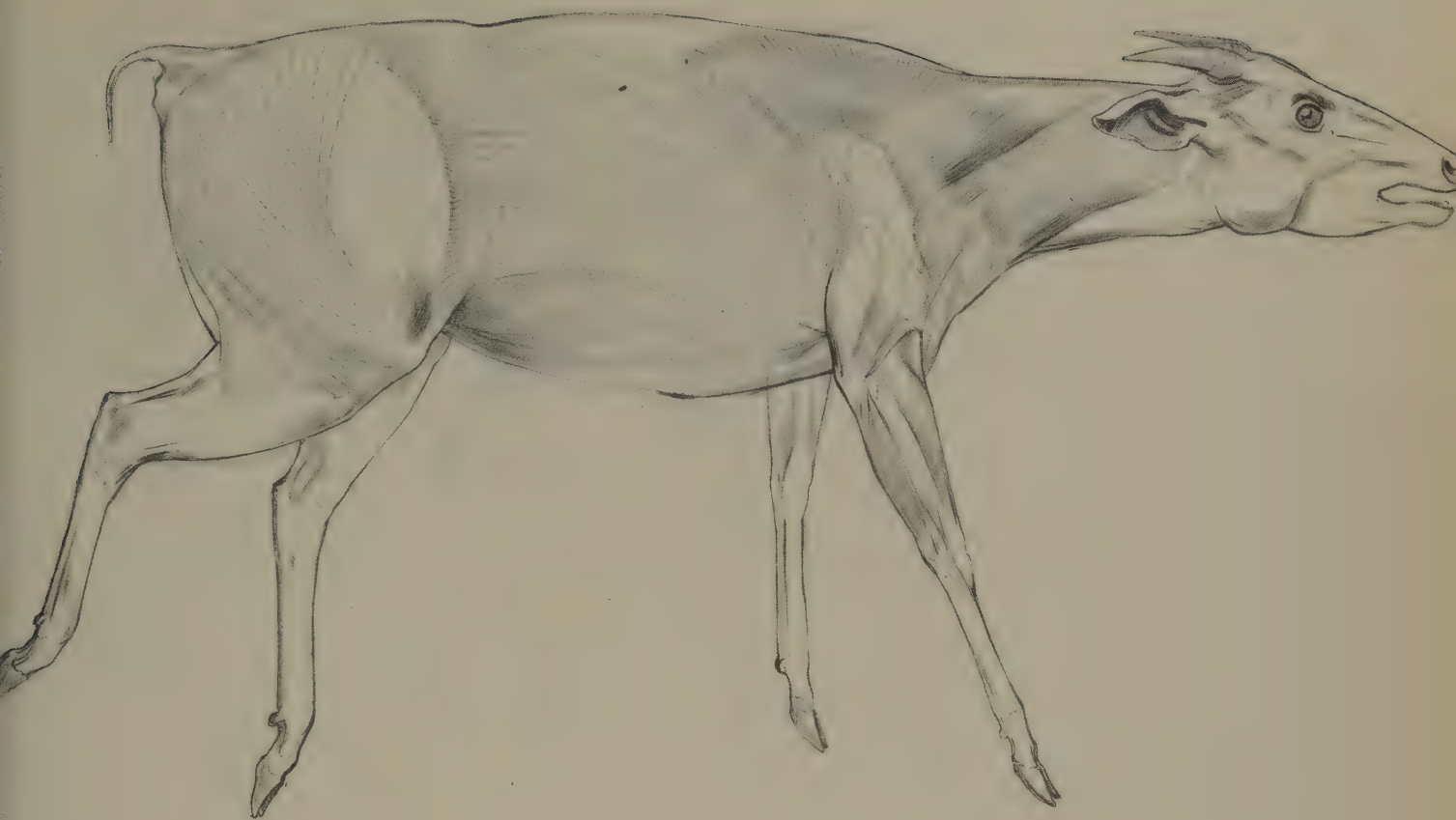


they are quite common. In one such valley I found six well-used resting places within a radius of some 500 m with many tracks and the light herbaceous growth had been heavily browsed by the duikers and also by gorillas, which like similar conditions.

The duikers feed on fallen seeds, fruit, berries and the bark of shrubs, fungi and ground moss, also on many of the smaller herbs. In Bwindi, they eat the berries of *Syzygium*, *Ekebergia* and *Podocarpus* and I found that they had been visiting the fallen trunk of a dead *Rapanea pulchra* tree and, in common with *Cephalophus nigrifrons*, had been nibbling the rotten wood. Although it was rather tasteless, the wood may have contained minerals.

In Gabon Gautier Hion *et al.* (1980) recorded 71% of the diet as fruit and 29% leaves. This was the highest ratio of leaves that they found in any duiker species.

I was told in this locality that both species of duiker also make seasonal visits to the Bwindi swamp, an extensive area of tussock bog. My own visits were mostly during the rains but I did disturb a female with a half-grown young on the edge of the swamp in September. The species is crepuscular but may have both diurnal and nocturnal activity periods.





In general behaviour these duikers are similar to the other species. They have a piercing whistle and animals have been reported to take up position on termitaries. This behaviour has territorial implications and if red duikers are any guide, one might suppose the animals in question to be males. However, both sexes are well horned and a female with a broken horn suggests that perhaps both sexes fight.

Foraging is usually a solitary occupation and each animal lies up on its own in a highly characteristic "form". This is usually at the base of some large tree, under a fallen trunk or in a very dense tangle and I found one that had tenanted an old pit-sawyers' lean-to as a shelter. In Bwindi and in Kalinzu forest I was told that the only time they were seen in greater numbers than two was during the dry season, when they visited the swampy valleys. As many as nine were seen by my informant in Kalinzu around a salt-lick area much frequented by elephants and forest hogs. I found a stump that had been used by a yellow-backed duiker for rubbing some 80 cm off the ground but found no evidence of glandular marking.

In Kigezi and Ankole this animal was traditionally subject to strict taboos and could not be touched or eaten. Forest hunters saw that it was aggressive and dangerous if netted or wounded. As a result, it enjoyed a large measure of protection until migration brought in people from other areas. I found the remains of a snared yellow-backed duiker that had been skinned and dressed in the forest, presumably so that the meat would not be identifiable when sold in the market.

Ansell (1960, 1964) thought that there was no fixed breeding season in Zambia but reported a lactating female in March and young in October and December. Ionides (1965) noted young in Kenya during January. Gestation is reported to be about four months (Jeannin, 1936) and a single young or occasionally two are born at yearly intervals (Asdell, 1964).

The fawn is born with a dark umber back and a strong reddish tint, particularly on the underparts; the sides are flecked. At birth the back is jet black and the adult colour is acquired only over some months. Captives have been recorded living nine years.



Bay Duiker
(Cephalophus
dorsalis)

Family
Order

Bovidae
Artiodactyla

Measurements
head and body

75—85 cm

height

56 cm

tail

10—12 cm

ear

7—7.5 cm

weight

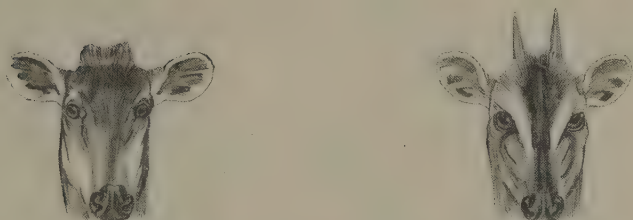
22 (14.5—24) kg

horns

4—10 cm

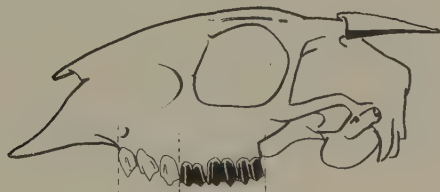
Bay Duiker (*Cephalophus dorsalis*)

This heavily-built red duiker has dark brown or black legs and a black midline along the back and belly, which varies individually in width and in the intensity of the black. The fur is very coarse in texture and the crest is poorly developed.



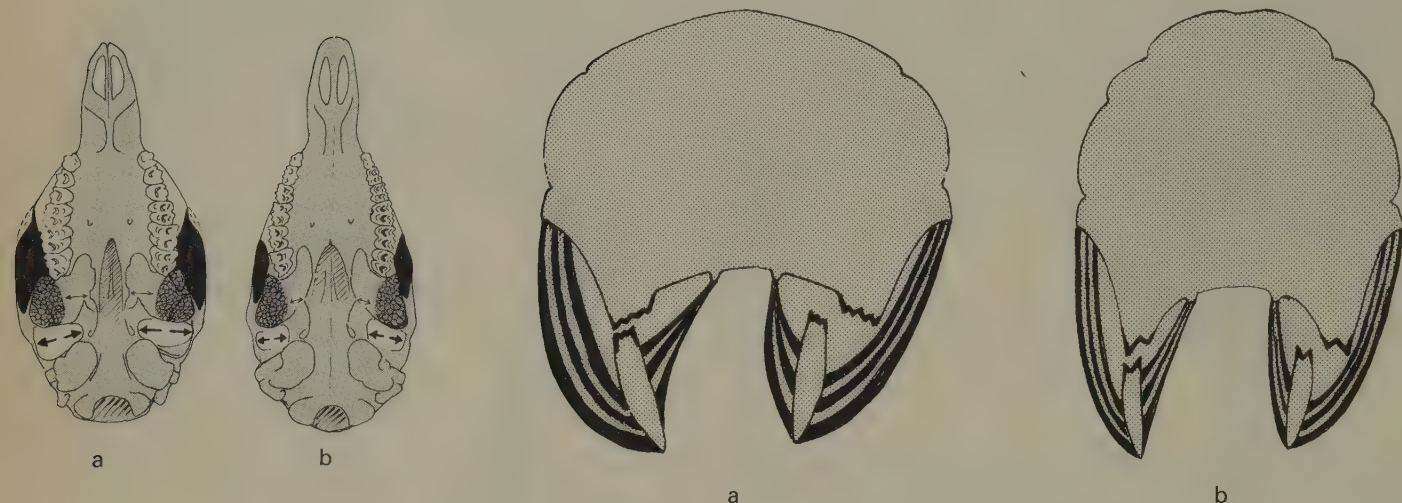
Frontal view of *Cephalophus sylvicultor* and *Cephalophus dorsalis*.

The head of this duiker has several notable modifications which can be related in various ways to a sparser, more difficult diet, to a very low density and to a nocturnal activity pattern. Unlike *C. callipygus* and *C. nigrifrons*, species of similar size and colouring, the braincase lacks a dense bony shield and the forehead is relatively less protuberant. The slender horns are strongly depressed and it is very unlikely that this species normally uses either forehead or horns in frontal clashes. The sharp, smooth spikes are more likely to be used as a stabbing weapon, without ritual, during the rare encounters of widely-spaced individuals.



The muzzle is extremely reduced and strongly tapered. The incisors are correspondingly small and the front of the mouth better adapted for a pincer action than for cropping. Partly because of the reduction of the nose, the forebrain and olfactory region appear to be disproportionately large relative to other duikers. This could possibly imply a more developed sense of smell or it may be an artefact of allometry.

Appropriately for a nocturnal species the eyes are proportionately bigger and more elevated in the skull (elevation of the orbits is partly responsible for flattening of the forehead in cross-section). Even more unusual, the lower margins of the orbit and eyes protrude on either side of the head to a degree that must improve bifocal vision. This outward flare of the eyes and their sockets is the product of inflation in the zygomatic bone but the benefits to vision are secondary to the need for enlarged attachments for the masseter and a wide lateral swing at the maxillary condyles. These developments can be correlated with the adoption of a tough diet and considerable expansion and specialization of the three molar teeth (see p. 17).



Above, left: comparison of *Cephalophus dorsalis* (a) and *Cephalophus nigrifrons* (b). Above, right: ventral view of *Cephalophus dorsalis* skull shows robust teeth, heavy masticatory muscles and wider traverse at the mandibular condyle. Schematic cross-section shows relationship of masseter and pterygoid muscles to the mandibles and tooththrows.

The unusually wide traverse of the lower jaw explains the very narrow channel of the choane and why the associated pterygoid bones are less flared than in other duikers.

Differentiation in function between premolars and molars became apparent to me in observation of a captive that lifted a sweet potato and retracted its lips while it opened its gape wide (a capacity increased by the shortness of the muzzle) and bit through the root with its premolars. Having dropped the main piece it chewed the remnant with its molars. Kurt (1963) watching carnivorous behaviour in this species also recorded the animal using the cheek teeth to break or tear pieces off a pigeon after which it chewed them. Kurt also noted that olfactory tracking and sniffing was a stereotyped preamble to feeding and this would accord well with the nocturnal habits and well-developed nasal area in this species.

Of the many fruits that fall to the forest floor not all are accessible to conventional duikers. Some fruit are too large to be easily bitten and some are too hard, fibrous or rough-skinned to be chewed with poorly developed masticatory equipment (see above). In addition to fruits such as those of *Treculia*, *Klaineodora*, *Strychnos*, *Irvingia*, *Myrianthus*, *Balanites*, *Elaeis* and *Chrysophyllum* spp. there are also edible stems and roots and a variety of low-level plants with tough, fibrous leaves. Large fruits are in general rarer than the smaller berry-like fruits but they are subject to less competition.

Dubost (1979) estimated that fruit measuring over 4 cm constituted only 5.43% of the fruit falling in a representative area of Gabonese forest. The existence of alternative foods, including animal prey, may help to buffer this duiker against occasional shortfalls in its main foods. Gautier-Hion *et al.* (1980) recorded 72.9% fruit, 26.6% leaves and traces of animal matter, flowers and fungi in the stomach contents of this species. Dubost (1979) comparing the distribution of captures of three species, *C. monticola*, *C. callipygus* and *C. dorsalis* in the same area of forest in Gabon found the latter much the rarest. In a total area of 70 hectares twelve captures suggested a density of about one *C. dorsalis* in 5.88 ha. *C. callipygus* was caught 16 times (one per 4.35 ha) and *C. monticola* was much the commonest with two animals per hectare.

Of twelve animals trapped by Dubost (1979) in Gabon seven were caught in the densest undergrowth. *C. callipygus* was more evenly distributed and *C. monticola* showed a distinct preference for areas that were less-heavily obstructed.

Dubost (1968) has described *C. dorsalis* as an inhabitant of mixed forest zones with dry and moist areas, and he records it from gallery forest, dense thickets and from the edge of plantations. He thought this was the most strictly nocturnal of the species found in Gabon and he found them sheltering within the hollows of fallen tree trunks. They are solitary outside the reproductive period and, when forced into flight, make a rapid getaway but for a short distance only. Rahm (1966) noted that a specimen killed in eastern Zaire had eaten the fruits of *Dioscorea* and *Klainedoxa*.

A duiker of this species has been seen to stalk, kill and eat the pigeons that came into its pen in the Zurich zoo, after which it always groomed itself. Digestion of the meat was found to be complete. If this animal provides an indication of actively predatory habits then the acquisition of bifocal vision might be of functional significance even if animal matter only constitutes part of its diet. I have seen *C. callipygus* feeding in the midst of a flock of forest guineafowls and it is conceivable that a predator masquerading as a harmless ungulate might be as effective as Aesop's wolf in sheep's clothing.

This animal has been kept in zoos and has successfully hybridized with the striped duiker, *C. zebra*, in Frankfurt. Fradrich (1966) noted that the hybrids resembled their sire, *C. dorsalis*, in having a nocturnal activity pattern and that their voice was also similar to his.

Within the main lowland forest block, *C. dorsalis* is widely distributed and it is reported to prefer dense growth. Happold (1973) described its West African distribution as patchy but locally common. Rahm and Christiansen (1963) noted that it was rare in montane areas of the Kivu province but more common on the lower slopes and in lowland forest.

This species is included in our fauna on the basis of the skin of an animal from Bwamba which was reported to have been trapped in gallery forest just below the north western foothills of the Ruwenzori Mountains, an area which is now so densely cultivated that the species is unlikely to survive there.



**Bush Duiker,
Common
Duiker
(*Sylvicapra
grimmia*)**

**Family
Order
Local names**

Bovidae
Artiodactyla

Nsya (Kiswahili), Ensa (Runyoro), Nthia (Kimeru), Thiya (Kikari, Kikuyu), Wapala (Kizigua), Empeewo (Luganda), Unuma (Runyankole), Sumbuda (Kipare), Ngururu (Kiamu), Kinamori (Kichagga), Ikhisi (Luhya, Lugisu), Amuri (Karamojong), Lacek (Lwo), Amori (Ateso), Yamwet (Sebei), Ngemuyenik (Elkoni), Cheptirkichoi (Kalenjin).



Bush Duiker, Common Duiker (*Sylvicapra grimmia*)

Measurements head and body

95 (70—105) cm males

100 (90—115) cm females

height

60 (45—70) cm

tail

11 (7.5—19.5) cm

weight

18.5 (11—21.5) kg males

20.5 (12—25.5) kg females

horns

11 (7—18) cm

Note: Average weights vary regionally but females are between 2—4 kg heavier than males.

Races

Sylvicapra grimmia roosevelti

Sylvicapra grimmia orbicularis

Sylvicapra grimmia deserti

Sylvicapra grimmia nyansae

North-West Uganda

Tanzania, Central Kenya

East Kenya, North-East Tanzania

Uganda, West Kenya.

S. g. roosevelti

North Savanna form. Smallish, short-eared (9.5 cm). Drab grizzled, sandy grey with off-white underparts, dull leg markings.

S. g. orbicularis (*uvirensis*, *hindei*, *altivallis*, *altifrons*, *ocularis*)

East African form. Larger, long-eared (11 cm). Buff-yellow with white underparts, conspicuous leg markings.

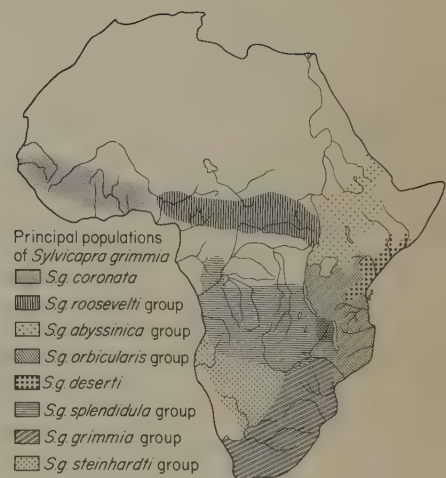
S. g. deserti

Eastern form adapted to semi-arid habitats. Long-eared, pale buff with white underparts. Indefinite leg markings.

S. g. nyansae (*lutea*, *lobeliarum*)

Intermediate forms from overlap zone. Shortish ears. Tendency for grizzled grey hindquarters and more ochraceous forequarters. Variable leg markings.

NOTE: High altitude isolates, “*altivallis*” and “*lobeliarum*” have longer, darker coats than their lowland parent populations.





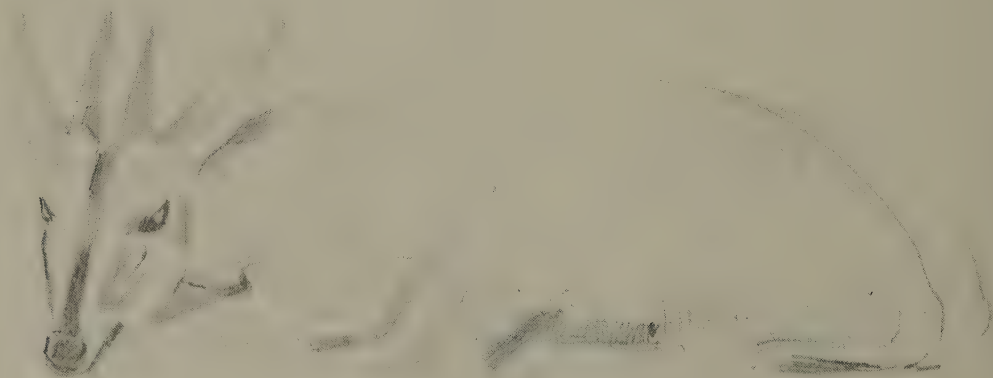
The bush duiker is more slender and larger-eared than the forest duikers, features that probably correlate with less tangled habitats and greater exposure. Indeed within the species itself the ears vary in size, the smallest belonging to duikers from the Northern Savannas while East African duikers have larger ears and the largest (up to 14.6 cm) come from very dry open habitats in the Kalahari.

Unlike the other duikers, *Sylvicapra* can run fast for some distance and it is probably improved gaits and longer leg proportions that explain why it carries its spinal column straight and square to its long legs. Naturally longer legs require a longer neck and this may have the added advantage of elevating the levels within which the species can feed.

Living in drier and relatively more exposed habitats than its relatives, the grizzled grey or tawny colouring is adapted to be as inconspicuous as possible. It is as dependent as the other duikers on freezing or crouching to escape detection unless it is discovered, in which case it will dash for the nearest thicket. The white-lined tail disrupts an otherwise cryptic colour scheme but this is conspicuous only when it is flashed. At close quarters the black and russet forehead, delicately marked face and ears and dark-stockinged feet are striking.

A high degree of individual variation encouraged nineteenth-century-taxonomists to list over forty subspecific names but variability might also provide the basis for a rapid adaptation by local populations to very different levels of humidity and temperature, particularly levels of humidity and temperature, particularly as it is the colouring and length of the fur that varies most. Duikers from moister areas are dark while lighter animals are found in more arid parts and those from the cold alpine zones of some East African mountains generally have the longest coats.

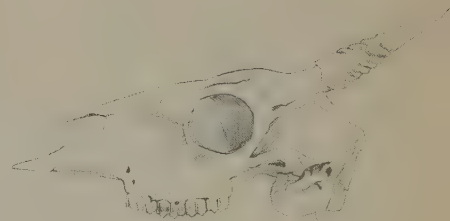
There are, however, recognizable traits in geographic regions. For example, rather plain, tawny duikers occur between the eastern coastline and the Rift Valley lakes and another yellowish population occurs in Senegambia. The Northern Savannas and woodlands from the Niger to the Nile are inhabited by a small heavily grizzled or vermiculated grey duiker, and grey grizzling is equally characteristic of duikers living between the Cape and Zambia.





As with so many savanna species, climatic changes seem to have separated populations and then brought them together again. The formerly forested areas in Uganda and western Kenya have probably been colonized by duikers coming from both latitudes, which would explain the intermediate and somewhat variable patterns found in this “overlap” region.

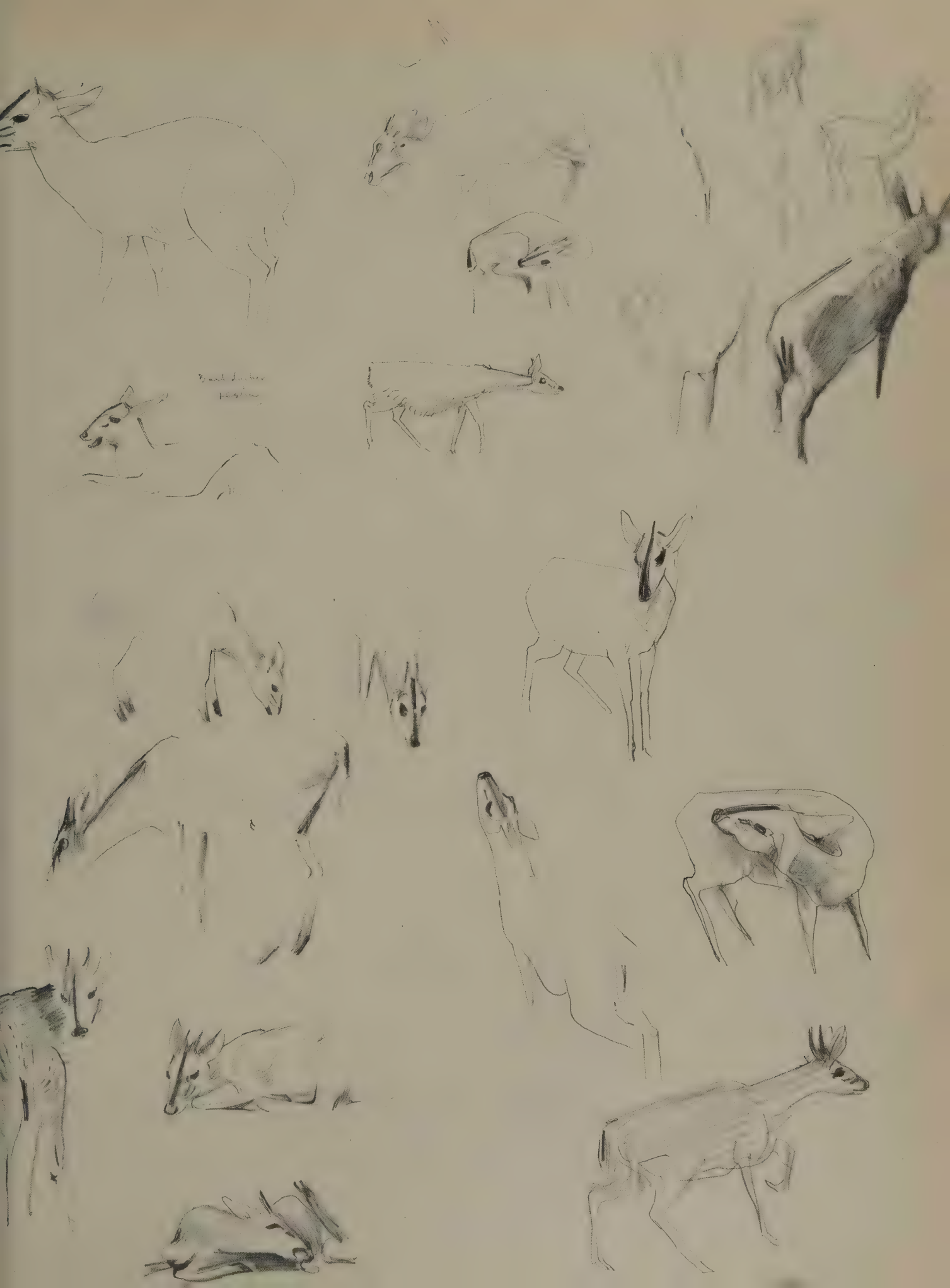
Widely distributed in Africa, bush duikers do not inhabit deserts or the very hot habitats bordering the arid zones, nor do they occur on open plains or in dense forests. They are generally present in savanna and woodlands at all altitudes but their abundance varies a great deal. Density is probably determined by the food available, by the type and amount of sheltering vegetation and by certain minima in the size of their territories, which may in turn be influenced by food resources, shelter and visibility. Forest duikers and other competing ungulates might also narrow their choice of habitats and it is interesting that this species has been the principal beneficiary of some of the Tse-tse Control Department’s efforts to exterminate wildlife.



In Rhodesia and Uganda many tens of thousands of large mammals have been shot annually over extensive areas, yet in both countries there is evidence that intensive hunting fails to remove more than the annual increment of duikers and the subsequent ecological changes appear actually to benefit them (Wilson and Roth, 1967). Furthermore, Riney (1963b) showed that duiker populations increased in the presence of hunting and in Zambia Child and Wilson (1964b) thought that a population was still expanding two-and-a-half years after hunting had ceased. Bush duikers also continue to flourish on cultivated land and even in suburbia. The principal causes of the duikers' success are likely to be an increase in the amount of cover and a superabundance of food following the destruction of the larger ungulates and the removal of their influence on the vegetation.

Except for small quantities of fresh green shoots, duikers never eat grass but their diet is varied, quite frequently including animal foods as well as the browse and fruit which are their staples. Leaves and shoots of dominant bush species are commonly recorded, i.e. *Acacia*, *Combretum*, *Terminalia*, *Cissus*, *Diplorhynchus*, *Sclerocarya*, *Ficus*, *Dichrostachys*, *Ipomoea*, *Solanum*, as well as others. Many fruits are eaten, notably the pods and seeds of Caesalpiniaceae and Mimosaceae, the fruit of *Ficus*, *Solanum*, *Strychnos*, *Parinari* and *Balanites*; in southern Africa they are so partial to the fruit of *Pseudolachnostylis maprouneifolia* that this small tree is known as the duiker bush. The flowers of *Kigelia*, *Lannea* and *Dolichos* are eaten when they fall to the ground and the activities of monkeys, birds and fruit bats often provide them with an abundance of fruit, flowers and leaves. The resin of *Mimosaceae*, *Combretum* and *Diplorhynchus* is gnawed; bark and various roots, bulbs and tubers, which are exposed by their sharp hooves, are chewed. Cockroaches, caterpillars and other insects are occasionally recorded, also snails and mushrooms. The duiker also eats vertebrates and carrion, notably frogs, birds and small mammals. Wild duikers have been seen to attack small rodents and birds up to the size of an egret while captives commonly attack poultry and young rabbits. The animals chew up the flesh or skulls of their victims after biting and pulling at the head and sometimes lap the blood. Hofmann (1973) watched one stalk and swallow a striped mouse in the Aberdares and he found small bezoars of what was thought to be rodent hair in the stomach of duikers shot in Kenya; he also sieved out soil and fine pebbles from many of the stomachs. Hofmann remarked that the very large thin-walled ruminoreticulum has primitive features and is adapted to bulky, heavy food and he predicted that this species could not exist for long on grass roughage. Dunbar (1978) noted that Ethiopian duikers spent 35% of their time feeding coming out into the open to find herbs which accounted for 87% of their diet, shrubs and bushes 11% and grass the remaining 2%.

Bush duikers get their water needs from their fodder and captives often ignore water troughs. As the only savanna-dwelling duiker, the animal's ability to survive a drier regime than *Cephalophus* is interesting. Their strategy may lie partly in a great diversity of foods (most of which are found reasonably moist) and also in restricting their activity to the cooler, moister early mornings, evenings and earlier part of the night, lying up for the heat of the day in shady retreats.

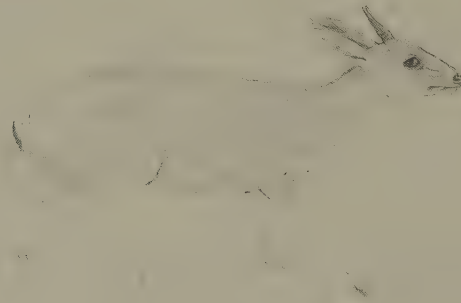


Small sketch of a deer head with the handwritten text "Small sketch of a deer head" written next to it.

Verheyen (1951) observed that males and females tend to choose rather different resting places. The latter are lower and better hidden, often close to a tree trunk or log, and the animal frequently returns to the same place unless disturbed. A male, instead, may use one of several well-spaced resting places, which tend to be more elevated, perhaps on the slopes of a bushy termitary, valley or hillock, places which appear to offer a better surveillance of the surroundings. When food trees are fruiting, the resting places are often marked by small piles of seeds which are spat out in the course of rumination. The difference in choice of sites for resting may be connected with territorial behaviour. Other signs of territorial behaviour are secretions from the pre-orbital glands, which are smeared on branches, trunks, rocks and other landmarks. Deposits are most concentrated between 18 and 28 cm off the ground but appear to be limited to surfaces between 13 and 35 cm high. They also make dung deposits but this habit is not as well developed or consistent as in the neotragines.

An adult male is intolerant of all other males but has a loose association with one female which lives in the same territory. Except for a brief period while the immature young accompany their parents no more than two animals are seen at a time. Like the male, the female drives off other females with butts and chases. When a male sees another in its territory it stalks towards it and charges. The intruder generally runs but free-ranging animals confined by perimeter fences have been seen to evade their pursuer by an abrupt jink to the side and then lie down (Root, personal communication).

When males fight they lower heads and forequarters close to the ground and spar or jab at one another with their horns. As they become more excited they may utter a loud wheeze and make short threatening jumps, Sikes (1958) described them pronking as well as fencing with the horns and she noticed a strong smell emanating from two fighting males, which she ascribed to the pre-orbital glands. At the greatest intensities the mouth froths, eyes roll and the dodging and manoeuvres become very fast. Root has seen opponents rush together and tilt their heads sideways to stab or cut long scratches along their opponents' side. When one is wounded it may try to escape or else lie cowering on the ground (Sikes, 1958).



When a female first rouses the interest of a male she tends to flee and the early stages of courtship are a prolonged and noisy chase. In captives the pair run circuits around their pen and in the wild this presumably takes place within the bounds of the territory. When the female has tired of

running, the male blocks her path with a lateral display. He walks somewhat sideways towards her on his hoof tips and makes slow ritualized threat movements with his horns tilted towards her. The submissive female is approached by the male, who rubs the sides of his face against hers and she may respond by licking his face and glands. Sikes (1958) described the secretion pouring from the male's glands and thought that the two animals then looked as though they were drugged.



After mutual face grooming and smelling of the genitalia the male attempts to mount; after repeated circlings, groomings or chases he eventually succeeds in copulating. The male attends his mate very closely for several days and the female sometimes appears to invite chases, rather as a dog does, by lowering the chest in a brief mock challenge.

Estimates of gestation range between four months (Stevenson-Hamilton, 1912) and seven months (Wilhelm, 1933). Mentis (1972) mentions two estimates of five-and-a-half months. Ansell (1963) has reported a female giving birth at the age of one year. Several observers have thought that two young may be born in a year, which suggests that a shorter period is the more likely.

Only one young is born at a time and Child and Mossman (1965) have noted consistent implantation in the right horn of the uterus. Young are born at all times of the year in Zambia (Wilson and Clarke, 1962) but it is possible that there is a prolonged birth peak during the rains in Tanzania (Harrison, 1936). Numerous instances have been found of pregnant mothers having sucking young in attendance betraying a post-partum oestrus. Sikes (1958) described the birth in detail.

The young are precocious and can run within a day of birth; however, they lie up for long periods in dense vegetation between sucking. The mother's twice or thrice daily visits are brief and the youngster may change its station periodically. The coat of the newborn bush duiker is darker and more woolly than that of the adult but growth is rapid and the beginnings of adult coat colouring are apparent before the animal is two months old, and at six or seven months it is adult sized.

While still lying up the young sometimes suck their folded knee and the knee remains a focus of interest in adult interactions, suggesting that glands may be present in that region.

If a juvenile is caught it bleats very loudly and this has an instantaneous effect on all neighbouring adults of both sexes, which come rushing to the spot. It is possible that lesser predators are butted or horned but when I have picked up a fawn the mother, closely followed by a male, ran up at full tilt only to pass by and disappear into a bush, repeating the charge at the next bleat.

Hunters call up adult duikers by imitating this bleat and it is quite common for the call to attract carnivores such as hyaenas or leopards. Wild dogs have been found to be an important predator in the Kafue Valley, where duikers are very numerous, and Wilson (1966c) included most of the larger African carnivores, martial eagles and pythons as predators of the bush duiker; (one python was found dead from internal perforations inflicted by the dead duiker's horns long after it had been swallowed).

The role of duikers in the transmission of trypanosomiasis has been investigated by Keymer (1963) in a study of their blood protozoa. Once the larger ungulates or the woodland cover have been destroyed tse-tse fly populations are unable to sustain themselves on the blood of duikers, however numerous, although they are one of the hosts in an undisturbed woodland community.

This species is sometimes a nuisance in vegetable gardens and is hunted both in reprisal and for its flesh. The horns are widely used as a pendant

or as a charm against evil spirits, but according to Watson (1942) duikers are believed to be beasts of ill omen in Teso and Karamoja, bringing failure to hunting parties and sterility to women who are unfortunate enough to set eyes upon one.

Duikers make popular pets but the males tend to become dangerous when adult. Lacking the public appeal of the larger antelopes they are rare in zoos but have been recorded living nearly 12 years in captivity.



Reduncines (Reedbucks, Waterbucks)

Reduncini

Genera

Redunca

Kobus

Species

Redunca fulvorufula

Redunca redunca

Redunca arundinum

Kobus adenota

Kobus kob

Kobus ellipsiprymnus

Kobus megaceros
and *leche*

Kobus ellipsiprymnus

Kobus kob
and *vardonii*

Redunca fulvorufula

Redunca redunca

Redunca arundinum

The edaphic grasses growing in swamps, flood plains, valley bottoms and other swamp areas are a rich source of food for herbivores. But Sump-lands are difficult to exploit, especially for small antelopes because of their fluctuating water levels, sticky soils and rapid growth of tall grass, which replaces accessible greenery with an obstructive jungle of tough stems. Where there are fires during the dry season this is an additional hazard resulting in the temporary loss of shelter and food but has the beneficial effect of promoting more accessible new growth. On alluvial soils the grazing is particularly nutritious and regrowth can provide pasture throughout the dry season so long as the water table remains high. During the dry season most valley grasslands are invaded by herds of herbivores coming in from the hinterlands. This annual invasion apart, exploitation of the sumplands has been a speciality of one bovid group, the reduncines.

Like the valley grasses on which they feed, these antelopes are moisture-dependent but only the lechwe remains permanently in the wet lands. (This species, which does not occur in East Africa, has swamp-adapted hooves like the sitatunga.) For the rest it is probably the need to accommodate great seasonal changes that has inhibited extreme specialization, both in limb proportions and skull structure and this makes the group unusually homogeneous. Most tropical grasslands would revert to woody growth in the absence of fire or exceptionally heavy grazing pressure (see Vol. I, pp. 38—40). The valley bottoms and some montane grasslands are the only exceptions, being maintained by peculiar soil and climatic conditions. Montane grasslands have a discontinuous distribution and are inhabited by the smallest of the reduncines, *Redunca fulvorufula*, which has evidently become especially adapted to coarse grazing and cooler climates in the uplands to which it is now restricted.

The living species are graduated in body size and in the length of their horns.

Species	Average body mass	Horn length
<i>Redunca fulvorufula</i>	30 kg	14—38 cm
<i>Redunca redunca</i>	45 kg	20—41 cm
<i>Redunca arundinum</i>	50 kg	30—45 cm
<i>Kobus adenota</i>	70 kg	40—54 cm
<i>Kobus kob</i>	77 kg	40—69 cm
<i>Kobus leche</i>	170 kg	50—92 cm
<i>Kobus megaceros</i>	190 kg	60—87 cm
<i>Kobus ellipsiprymnus</i>	200 kg	55—99.7 cm

It is significant that the smaller species tend to retain more primitive features than the larger ones but an examination of the reedbuck, notably *R. fulvorufula*, shows that all surviving species have evolved specialized or advanced characteristics. In limb proportions, body size, elaboration of the horns and territorial attachment, the mountain reedbuck is nearer to a generalized primitive bovid than any other reduncine. Its colonization of



Mountain reedbuck, *Redunca fulvorufula*.

uplands was probably the product of a dominant ancestral stock having extended its range into all types of grassland. Subsequently this lineage relinquished the lowlands to relatives that were larger and more advanced in most particulars. Early adaptation to and better tolerance of the climatic difficulties of such habitats enabled the *fulvorufula* stock to remain ascendant in the uplands. Contracting into a more exacting and specific type of range may explain why this species has become better adapted to a diet of roughage than its relatives (Hofmann, 1973). In bovid phylogeny the capacity to digest a more fibrous diet is generally regarded as a progressive adaptation; in the case of the mountain reedbuck it would seem to be the specialization of a relict form pushed into an ecological cul-de-sac. The mountain reedbuck is more rigidly conservative than any other reduncine in its attachment to a territory or home range, a primitive trait that is consistent with its smaller size, and these may be its major limitations. The mountain reedbuck's ability to digest very coarse grasses has probably improved its chances of



Kobus ellipsiprymnus.

survival in difficult habitats. Even so, in spite of its size it is sorely pressed by drought and poor grazing, especially in bad years and at high densities. This suggests that it is close to the outer limits of the reedbuck's ecological tolerance. The combination of superior digestive efficiency and smaller size is distinctly anomalous and implies that this capacity developed subsequent to the mountain reedbuck's ecological isolation.

If early reedbucks were to exploit extensive valley grasslands effectively, emancipation from such an extreme territorial attachment is likely to have been of greater importance than digestive efficiency because in the valley habitats good quality grass was to be had in superabundance. The height and nutritive value of the grasses change with the seasons; floods exclude animals from some areas in the wet season, drought and fires from others in the dry. This means that resident animals are exposed to food shortages or predation and so must move or at least alter their ranges. Quite modest increases in height and weight would be an advantage in the rank grasses growing in the valleys and longer legs are appropriate to animals that are exposed to danger or have to make periodic movements.

Some valley grasslands associated with major river basins have undoubtedly seen a large measure of ecological isolation in the past and with it isolation of local reduncine genotypes. I have already stressed that past climatic changes have provided a major mechanism for speciation in Africa (Preface and Chapter 4, Vol. I). Regional variations in the bodysize of reduncines could be predicted to have some correspondence with local reliability and abundance of forage. Even today several reduncine species show variations in the body size of regional subspecies; (in the absence of detailed quantified measures of the weight of subspecies, maximum horn lengths can be used as an indication of sub-specific differences. These are thought to have some correspondence with body size).

The figures below suggest that there may be some relationship between higher primary productivity (implied by more wet months) and body size (implied by greater maxima in horn lengths).

BOHOR REEDBUCK, *Redunca redunca*

Subspecies	Range	Average number of wet months	Range of horn length in top 16 trophies
<i>R. r. redunca</i>	Gambia to Togo	5—7	20.64—28.3 cm
<i>R. r. nigeriensis</i>	Nigeria to South-West Sudan	5—8	27.5—32.0 cm
<i>R. r. bohor</i>	Ethiopia	4—9	29.2—35.6 cm
<i>R. r. wardi</i>	East Africa	4—10	30.5—37.4 cm
<i>R. r. cottoni</i>	South Sudan	8—9	37.5—41.6 cm

KOB, *kobus*

Subspecies	Range	Average number of wet months	Range of horn length in top 16 trophies
<i>Kobus vardonii</i>	South-central Africa	6	49.5—54 cm
<i>Kobus kob kob</i>	West Africa	5—8	60—64.7 cm
<i>Kobus k. leucotis</i>	South-East Sudan	8—9	59—66 cm
<i>Kobus k. thomasi</i>	Uganda	8—10	62.2—69.2 cm

Environmental and body-size differences such as those observable in contemporary reedbuck, if sustained over great periods of time and in habitats separated by an equatorial belt that was sometimes heavily wooded if not forested, would have provided an adequate basis for speciation and subsequently a differential use of the catena such as can be seen today in the areas of overlap between *Redunca redunca* and *Redunca arundinum*. During the Pliocene kob-like reduncines also entered Eurasia and this too could have led to further speciation.

Because they exploit a superabundant resource, reduncine populations have the potential of reaching huge densities at times when conditions are

right for them (p. 370). They are also sedentary so that invasion of Eurasia is very unlikely to have been a "sweepstake" colonization but was rather the product of a climatic period during which favourable ecological conditions were very widespread and spanned the Arabian bridge.

It is, to my mind, an important priority for future research to make a detailed comparative study of reduncine social structures. Important parameters are a species' vegetation and grass height preferences, its capacity to exploit, withstand or mitigate the effects of inundation and/or drought, its heat tolerance and specific responses to variable population density. Every species of contemporary reduncine is capable of accommodating to crowding, if only on a seasonal basis, and the primary external pressures in favour of crowding are environmental. There is no evidence that very large reduncine herds are a response to predation, as there is for some of the tragelaphine species (see p. 150).

Because their food needs are less, the smaller species are better able to survive in areas that become drier or are more completely burnt out during the dry season. Thus the smallest species, *R. fulvorufula*, occupies the driest habitats but also has the smallest and most temporary aggregations. The larger species are predictably more dependent on fairly high levels of primary production—grass—being sustained throughout the year. Thus the large-sized lechwes occupy the wettest habitats and have the richest and most permanent food supply. Lechwe together with puku and kob also have the largest and most sustained groupings and it is probably reduced predation and rich but difficult grazing that help the former two species to achieve very high densities and large group sizes—they are reliant on water not only as a physiological necessity and the source of perennial grazing but as a refuge. Waterbuck also take to water when pursued by dogs or hyaenas and the reduncines' vulnerability to carnivores probably increases with size. Adult and juvenile waterbuck patently need the cover found along drainage lines and it is probably this need for refugia that explains the species' preference for mosaics of grass and thicket and puts an upper limit on group size. Such habitats can only shelter relatively small groups and predation may be a major factor in prohibiting waterbuck from congregating in the large concourses that are common for lechwe, puku and kob.

The absence of lechwe in East Africa may have been influenced by climatic vicissitudes and the rarity here of extensive flood basins where the swamps have never dried up. These most specialized of reduncines rely on keeping close to or within flood water margins throughout the year and to maintain their ideal environment they commonly move up and down the catena. Long- and short-term movements are general in the Reduncini, they can be a response to floods, suitable grazing, fire, drought or the loss of cover and there is evidence that the movements of some reduncine species may be influenced by the passage of large migratory herds of *Damaliscus lunatus*, *Connochaetes* and *Equus quagga*.

The scale of these movements varies from species to species and within a species it varies with the topography of the habitat and from year to year. For example, on the flood plains of the Nile both *Redunca redunca* and *Kobus kob* are constricted by floods during the wet season. At the end of the dry season drought forces both species to concentrate in quite different

areas (in the case of the reedbuck some tens, in kob hundreds of kilometres away).

Highly localized environmental pressures also determine density and most reduncine species appear to be unusually labile in accommodating their social behaviour to changes in density. How can this social flexibility be explained? It is undoubtedly facilitated by the absence of a sign-posted land tenure system.

Where populations become aggregated at high densities, however temporarily, most or all of the males tend to be non-territorial. This is so for *Redunca arundinum* (Venter, 1979), *Kobus kob*, *Kobus leche* (Lent, 1969) and *K. ellipsiprymnus* (Spinage, 1969d). Not only are conventional territories difficult to defend in a crowd but large numbers of females and young attract bachelors and shield them from aggression so that the latter tend to gravitate to overcrowded areas and swell the numbers.

Where bachelors gather into groups they typically adopt dominance orders based on size, age and hormonal condition. If mating opportunities occur in high density areas they are therefore likely to be monopolized by animals from the top of the dominance hierarchy. Reproductive privileges can be reserved by herding females and persistently driving other males away from them, as appears to be the case with *K. megaceros*. *K. leche* have harems but the small numbers of animals living in sub-optimal habitats in Botswana are, like low-density reedbuck, spaced out in territories (Lent, 1969). All reduncines are territorial at low densities but perhaps the most complex, certainly unique accommodations to high density are made by kob and these are described in that profile.

Relationships between ecological conditions, nutritional resources, seasonal and daily movements, varying home-range sizes, population densities and social organization are discussed in the following profiles but a great deal remains to be learnt.

The absence of functional pedal and preorbital glands and the lack of physical marking of the habitat by the reduncines is probably influenced by the large size or transient nature of their home-ranges but it is more likely to be determined by the homogeneous but constantly changing nature of the vegetation, the lack of landmarks and the impossibility of scenting the substrate except during the dry season.

A scarcity of landmarks in the reduncine's world has had to be compensated for by an unusual adherence to routine and a conservative attachment to localized, even if seasonal home ranges.

The emergence of reduncines as a distinct group was contingent upon their emancipation from a more primitive system of labelling the environment and their abandonment of stable demarcated territories is linked with another major characteristic of the reduncines in which size is also a decisive factor. This is the elaboration and lengthening of the horns.

The outcome of day-to-day contests between neighbouring territorial males is very largely predetermined in primitive bovids by the exact site of the confrontation because an established system is underpinned by massive scent-labelling of the territories. The dangers of fighting with simple spiked horns are mitigated by the small size and weight of the rivals, by elaborate appeasement behaviour and by ritualized displays. The form





Left and opposite: *Kobus ellipsiprymnus*.

and function of a weapon cannot be understood in isolation from its broader biological context, thus the horns of a primitive sedentary antelope are used relatively infrequently and are essentially a subsidiary element in an elaborate spacing system that relies very heavily on indirect assertions of dominance or possession by means of olfactory markings.

The physical movement of animals, even over limited distances increases the chances of males interacting. Seasonal or longer term changes that alter the relative density of animals also increase the level of male competition. When unlabelled land is directly and more frequently contested by less sedentary and heavier animals the physical assaults that result subject horns to completely new and different selective pressures. Both offence and defence in a heavier animal are better served by horns that are disproportionately thicker. An opponent's onslaught is more safely neutralized if there are hooked or corrugated surfaces and a wider splay to catch his horns with. Offensive engagements are more effective if the opponents can grapple

horns and then wrench and push one another's heads in a direct test of strength and vigour. I have already suggested that it was precisely this reorganization of the spacing system and appropriate changes in horn and skull-form that marked the emergence of reduncines as an identifiably distinct group (pp. 163—167).

There are as yet no good fossil skulls indicative of the earliest stages of reduncine evolution but males of late Pliocene reduncines from Pinjor, in India, have depressions in front of the orbits (but not the females) to show that preorbital glands were late in disappearing. Fragmentary fossils thought to represent reduncines have been found at Langebaanweg in South Africa and Dhok Pathan in India (both early Pliocene). The earliest fossil attributed to the Reduncini is a frontlet from six-million-year-old deposits at Lukeino in Kenya (Gentry, 1978a).

Confirmation of neotragine-type facial glands in the ancestry of reduncines is manifested in vestigial ante-orbital glands in puku, *Kobus vardonii*, but the group's primal condition is probably better extrapolated from the living mountain reedbuck than it can be from the currently known fossils. The animal is probably not a great deal bigger than the earliest ancestors and the size and shape of the horns show the barest degree of elaboration from the original slender spiked condition. Anatomy and behaviour also demonstrate the structure of the changes that transformed a neotragine-type ancestor into a reedbuck.



Mountain reedbuck,
Redunca fulvorufula.

Mountain reedbuck males engage their opponents with a powerful downwards nod or sideways sweep of the horns and the contestants' jousting and horn wrestling involves a fast succession of striking and parrying nods of the head.

These violent movements are powered by contractions of the *longus capitis* which is sufficiently large in all male reduncines to contribute materially to the bulging mass of the throat, (notably in kob and puku).

The attachments for this muscle, processes of the cervical vertebrae and the basi-occipital bone, are exceptionally prominent and the latter are commonly cited as a diagnostic characteristic of the Reduncini. The basi-occipital prominences develop on any antelope that uses powerful down-stroke movements of the head during fighting (or possesses forward hooks to the horn). The feature appears in hippotragines, the impala, other alcelaphines and the antilopine dibitags, *Ammodorcas*. (The association by some taxonomists of Reduncini with Hippotragini and Alcelaphini has been based on similarities in the shape of the basi-occipital and molar teeth, these are discussed in other profiles, pp. 15, 26).

The presence of reduncines in early deposits in India has suggested an Indian origin to several authorities, and Gentry (1978a) considered that boselaphine origins were likely. Recent discovery of the earliest fossil in Africa, if correctly identified, has of course undermined the idea of an Asian origin that was based on chronological priority alone and Thomas (1979) dates the emigration of *Kobus* out of Africa and into Asia at about mid Dhok Pathan, over five million years ago.

The origins and emergence of the reduncines become better understood when the ecological and behavioural significance of bodysize, skull and horn shape and the distribution and type of glands are taken into consideration. When specialist developments have been explained and their influence on form taken into account for both groups, the common origins of the reedbuck and the oribi become obvious.

I have already discussed the absence of pedal and preorbital glands in terms of abandonment of a territory-labelling system. This has not meant any loss of sensitivity to olfactory clues but these normally pertain to direct scenting of the animal rather than the environment. All species have enhanced waterproofing with sebaceous secretions that oil the entire coat and scent the animal very strongly, especially males. This undoubtedly carries information on sex and status.

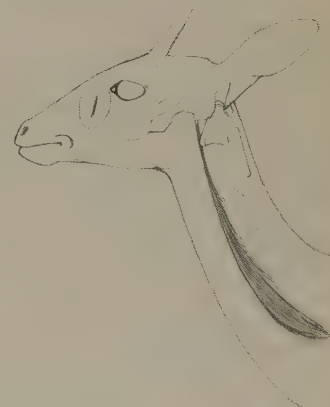
Labelling of the environment has not been totally abandoned, in that individuals can track one another by scent trails, and dung and urine deposits can, in certain circumstances, become very significant signals (see pp. 374, 393). Favourite lying-up spots may also be identified by scent and I have seen male waterbuck and reedbuck rub their greasy necks on branches. Nonetheless, in all reduncine species the concentration of scent signals on the animal is of major significance.

The link between mountain reedbuck and oribi is particularly explicit in their common possession of subauricular glands or "ohrenplaketten" which have been investigated in both species by Hofmann (1972, 1978), who described their extraordinary anatomical structure and stressed that the glands are effectively identical in both species.

In the oribi the ear patch augments an exceptionally elaborate barrage of scents and its function is further discussed in the profiles of the oribi and reedbuck. In reduncine species ear glands appear to have some correlation with spacing density. An ephemeral scent signal broadcast over



Kob, showing bulk of longus capitis in relation to head and neck.



Longus capitis muscle in top: reduncine (kob); below: neotragine (oribi).

a wide area from a single source can serve more than one purpose when authors and recipients of the signal are spaced-out members of a relatively sparse society but such signals merely become confusing at high densities. Appropriately, kob and lechwe, which live in large herds, do not have functional ear glands.

The relative importance of olfaction, vision and sound has been assessed in kob by Leuthold (1967). His conclusions, which probably apply to all reduncines, are that individual recognition, particularly between mothers and their offspring, is probably based mainly on scent clues: for the new-born young both olfactory and visual signals take precedence over vocal ones.



Mountain reedbuck, *Redunca fulvorufula*.

In adult life, however, sound may assume more importance, particularly in relation to social and territorial behaviour. Foot-stamping, which is characteristic of many antelopes, is rare in reduncines although it has been observed in kob on open ground. Ritualized leaping, which is particularly characteristic of reedbuck is combined with whistling and a distinct popping noise which is made by the inguinal glands. During leaps, scent is likely to be broadcast because the popping is the result of air movement within the inguinal scent-pouches.

Ritualized leaping and prancing is commonest in young male and female reedbuck and the leaping gesture, the popping and the whistling might

convey various information to another reedbuck. The flashing of raised buttocks is not purely an artefact of the jump. In some circumstances it may serve to identify the species, in others the age and sex class, but it is also possible that it signifies appeasement. In the kob ritualized jumping occurs more rarely but females may whistle after copulation and submission or dominance, indicated by a slightly raised or lowered rump, alters the line of the back which is visible even at a distance and in a relatively immobile animal.

There are other visual signals; when a male displays aggression he retracts and bunches the neck, lifts his nose or horns in the air and takes slow



Male and female kob, *Kobus kob*.

measured paces with hunched shoulders. In confrontations rivals circle one another with rolling eyes and intermittent horning of the vegetation or soil and contests may culminate in a fight. Females may also be herded or courted with typically aggressive or intimidating gestures. In reedbuck, kob and waterbuck there are white circular or semi-circular patches on the throat and contrasting leg markings which advertise the size of the horns and the thickness of the throat (which is due to hyper-development of the *longus capitis* muscles). In *Kobus vardonii* and *Kobus leche* the throat is white from chin to chest and in *Kobus megaceros*, the Nile lechwe, sexual dimorphism reaches its apogee in the reduncines. This species also illustrates the role of the habitat in determining the structure of a visual signal. A male that is not mature has no hope of keeping off numerous rival males and controlling singly a harem of up to 80 females—all chest high in water and swamp grasses. Visual advertisement of relative maturity is signified not only by horn length but also by darkening being progressive with age, turning from sandy fawn to dark chocolate or black. The saddle of the neck grows lighter, thus the dorsal colouring achieves maximum contrast at about the same time as the horns reach their fullest development. Not only are the pied forequarters more conspicuous but the neck saddle acts as a visual foil for the horns, allowing an easy assessment, even at some distance, of their relative horn size. Markings are dorsal because the animals lower surfaces are normally hidden and this age-graded colour code culminates in an extreme visual contrast which must reduce ambiguity and thus limit competition to a relatively small cadre of adult males in prime condition.



Inguinal glands in *Redunca redunca*.

Within this cadre status is continuously changing as males challenge for control of female groups. Only the strongest can hope to monopolize the largest harems, but even so dominant animals are soon exhausted and replaced. On the periphery of a local population unit an inferior or maturing male may temporarily control a small group or single females. Other males are sometimes tolerated by a harem-master but their numbers are limited to three or four animals, each strictly graded by colour and horn length. In both Nile lechwe and white-eared kob the pied males are clearly guided by sight as they gravitate towards one another. In this way they are able to identify, challenge and fight among themselves with minimal disturbance to the rest of the herd.

Saving the energies of both males and non-combatants could therefore be as important a factor in favour of colour dimorphism as its more obvious function of advertising displays such as the ritualized head-to-shoulder tosses that characterize *K. megaceros*. Since a major deterrent for conspicuousness is predation, it is significant that Nile lechwe are almost completely secure from attack by carnivores. Likewise, the equally conspicuous white-eared kob live on plains where there are exceptionally few large carnivores.

The importance of age-graded bachelor hierarchies in all social reduncines has already been stressed; in waterbuck and southern reedbuck bachelor groups tend not to exceed seven animals (see p. 388).

Oestrus is betrayed in the urine of females but several species may also indicate their condition through the exudates of the ear gland. Interest in oestrus is often quite intense in other females and homosexual mounting may occur. In most reduncines and some other antelopes the excretory posture and urinary pheromones of one female often tend to stimulate other



Redunca redunca.

females. In the kob this tendency is synchronized in time and place to provide the basis for a unique form of mating ground.

Young reduncines are born after a gestation of seven or eight months and they become imprinted during the first few hours. They are "hiders" and lie very close for the first few weeks of life. Close bonds with the parent seldom last much more than six or seven months. A curious difference has been reported in the pattern of juvenile independence in reedbuck species. In *R. redunca* there is the usual sequence of male offspring being driven off at an early stage by the father; in *R. arundinum* female offspring leave before the male, implying a greater tolerance of male offspring in this species. The reasons for this difference are unknown.

As the major bovid lineage adapted to valley grasslands the reduncines must be considered a major resource. They offer considerable potential for rational exploitation, having the fastest conversion rates of any bovid, very acceptable meat and hides and relatively insignificant disease problems. The potential for cropping kob in North-western Uganda was investigated by Bindernagel (1968) and its viability proven. Political events submerged his proposals, which deserve to be resuscitated. Both kob and puku would be amenable to forms of intensive management in which the distinction between farming and cropping might be less sharp than it is for more difficult species.

Large populations of kob and other reduncines are unlikely to survive unless their potential for sustained-yield cropping is realized because they occupy habitats with a high priority for agricultural or livestock development.





**Mountain
Reedbuck
(*Redunca
fulvorufula*)**

Family

Bovidae

Order

Artiodactyla

Local names

Tohe ya milima (Kiswahili), Ameriondet
(Sebei), Ekordareng (Karamojong),
Bongwe (Kikuyu), Esaste (Masai).

**Measurements
head and body**

110—136 cm

height

72 (65—76) cm

tail

20 cm

weight

30 (21·8—37·6) kg males

29 (19—35·2) kg females

horns

14—38 cm

Mountain Reedbuck (*Redunca fulvorufula*)

Race

Redunca fulvorufula chanleri

Smallest of the reedbucks, this species has a soft woolly coat of a somewhat greyer tone than that of the common reedbuck. The eyes and their sockets are peculiarly prominent and there is a black glandular patch under the ear which, like that of the oribi, serves as a scent dispenser (Hofmann, 1972). It has a conspicuous bushy tail with a white underside. This species is agile over very broken hilly country but, being of similar proportions to other reedbucks, is unable to negotiate the boulders and cliff faces that a klipspringer can.





The distribution of this species is unusual in that it occurs on widely separated mountains in South Africa, Ethiopia, East Africa and Cameroons. Although there are extensive areas of highland with apparently suitable habitat between Mt Hanang (the southern limit in East Africa) and the southern African population, these areas are occupied by *Redunca arundinum* which suggests that this species may be a direct competitor while *R. redunca* is not (see map). It is also possible that its strictly sedentary habits both inhibit rapid dispersal and render isolated populations vulnerable to extermination during prolonged periods of drought.



Mountain reedbuck are commonest on grassy mountain ridges from 1,500 m upwards; they also live in rocky broken country on small outcrops and on volcanic lava flows and cinder cones, where they may be seen in company with klipspringer. On Mt Kilimanjaro they have been seen as high as 5,000 m on the rocky moorland screes, where they are exposed to great extremes, night temperatures drop below zero with frost and snow, while the day is often very hot. To escape this heat mountain reedbuck tend to seek out well-shaded retreats in long grass or under bushes during the day.

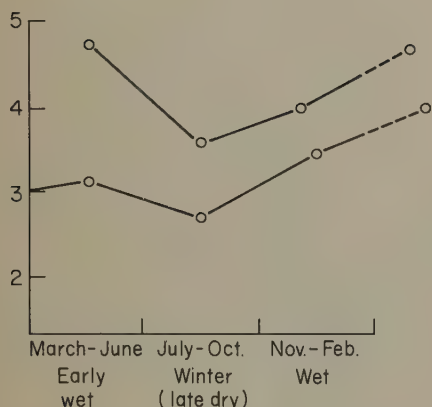
Soils, in most areas of its range, are well-drained and in volcanic areas tend to be ashy, fertile and well mineralized but prone to desiccation in the dry season. The animals will use plateaux or flats to graze or rest but nearly always retreat to the hillsides when disturbed. Irby (1976a) observed mountain reedbuck in vegetation types ranging from alpine moorland to tropical woodland, the common denominator being a ground cover of grasses. At Kekopey ranch in the Kenya Rift Valley, where there is an exceptionally high density of animals, they use the ecotone between slopes wooded with *Tarchonanthus camphoratus* and other shrubby bushes and open grassy valleys. In this area, Irby determined that *Themeda triandra*, *Hyparrhenia* and *Cymbopogon pospischilii* were the favoured grasses, *Bothriochloa insculpta* and *Enneapogon schimperanus* were taken in proportion to their occurrence while dominant species such as *Cynodon* were taken in lower proportions to their abundance. Virtually no non-graminaceae were eaten.

Mountain reedbuck graze selectively, wherever possible choosing the softest and greenest parts and Irby found leaves and sheathes in a ratio of nine to one of stem. The protein content of their food in this area remains well above the 7% maintenance level as established by Blankenship and Qvortrup (1973).

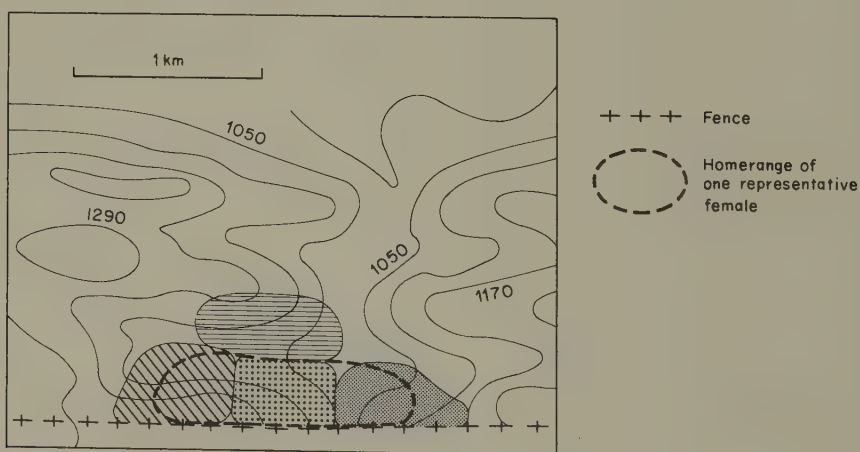
Some populations of mountain reedbuck appear to be able to manage without surface water for many months, but Irby (1975) has documented very pronounced seasonal variations in condition and weight, with males losing up to 41% and females up to 24% carcass weight in the southern African winter. Where water was available, Irby (1976a) estimated that animals drank once every nine nights during the dry season or, if they were active during the day, every other day.

There is great individual variation but more animals are active in the early morning and late evening, and Irby only recorded complete inactivity during the early afternoon. Although he found similar patterns in southern Africa during the wet and early dry seasons, daylight grazing increased during the late dry season when grass was dry and sparse; he also found a trend towards increased daylight activity after moonless nights in the late dry season.

Seasons have some influence on group sizes in southern Africa with somewhat smaller groups forming in the late dry and the largest average sizes occurring in the early dry season (see margin). In East Africa, groups number between three and six animals but larger temporary aggregations do very occasionally form. Simon (1960) has reported seeing more than 50 in the Chyulu Hills, which is a choice habitat for this species. Females with their young form small parties numbering two to eight. In areas of high density small groups of young males gather in bachelor groups. The females and their young live within the territories of single resident males. The size



Mean group size for *Redunca fulvorufa* populations in South Africa 1970-71 (from Irby, 1976).



Territories of three mountain reedbuck males "stacked up" against Loskop Dam Nature Reserve fence, with home range of one representative female indicated (from Irby, 1976).

of territories is apparently influenced by the relative population density in a locality. For example, Irby found an overall density of five to seven animals per sq km in southern Africa and the mean area of five male territories in the Loskop Dam Reserve was 28 hectares. At Kekopey ranch in Kenya, Blankenship and Qvortrup (1974) estimated an average of eleven animals per sq. km and Irby (1976a) studying these animals for seven months found occupation areas of 10—15 hectares. The fourteen groups observed included two composed of males. The 100 ha basin of a horseshoe-shaped volcanic crater contained ten groups and the rim of the crater apparently delineated territorial boundaries. Female home ranges in the Loskop area ranged from 36 to 76 hectares with an average of 57 hectares, but five collared females moved within an average area of 37 hectares which Irby considered to be the minimum size of a range.

Detailed records of the movements of known animals allowed Irby (1976) to plot the territories of five Loskop males and to determine minimal home ranges of five females from the same locality. These show the tendency for territories to range from hill-top to valley but hard up against the Reserve boundary fence he recorded smaller territories, which he aptly described as "stacked" up the valley slope (see diagram opposite). Summarizing his conclusions about density, Irby (1976a) wrote

"Density estimates for mountain reedbuck populations showed a narrow range and indicated a homogeneous spatial distribution of individuals within a population. The territorial social organization of mountain reedbuck did tend to spread males over all available hilly terrain, but the territories of males and the home ranges of females were easily compressed. Mountain reedbuck are sedentary animals so each slope or hill within an area of suitable habitat harbors a separate subpopulation. Each population is exposed to a different set of habitat conditions. Nutritional levels, cover conditions, predator impact, and burning intervals which determine relative success or failure of reproduction in each subpopulation can be radically different at distances of less than 1 km in mountainous terrain."

The territorial male tolerates juvenile males up to the age of about six months and finally expells them at nine to fifteen months. It is during the period leading up to and after the expulsion that juvenile males are most exposed to stress, malnutrition, disease and predators, and an even juvenile sex ratio becomes altered in many localities to one in which there are two or even three females to every male.

Broken tips to the horns and other signs of damage indicate that fighting can have serious consequences for young males. Both adults and juveniles are limited by their sedentariness, for example, Hofmann (1973) noted that several groups at Kekopey lived within one square kilometre over a period of five years. Irby (1976a) saw low-quality food in the dry season as the major limiting factor; he noted generally low parasite loads, marginal competition from other major herbivores and relatively light predation but he stressed that during droughts predation, parasitism and disease remove weakened juveniles and lambs that could otherwise have survived until the quality of the range improved.

The major predators are jackal, leopard, caracal, serval cat, hyaena and probably baboon, wild-dog, cheetah, lion and python in some localities.

Irby identified some seventeen helminth parasites, at least four ticks, lice and the parasitic fly *Strobiloestrus*, the larvae of which develop under the skin and are most frequent in immature animals during the wet season.

Territorial males are very reluctant to leave their territories, yet they use no very obvious means of marking them. The gland below the ears and the inguinal glands might diffuse scents that are perceptible to other reedbuck but their distribution must be incidental to the animals' daily movements.

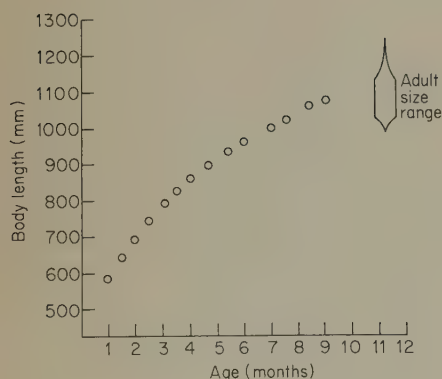
The only display observed by Irby consisted of an alert posture, stotting or stiff-legged jumping which is combined with short whistles. Longer whistles, shriller than those of the larger reedbuck species, appear in similar circumstances and, as Irby remarked (1976a), their use as an advertisement of territory can seldom be separated from their apparent function as warning calls. The white underside to the tail is also flared during disturbances or excitement, and probably acts as a warning signal too. A slow version of this gesture appears during courtship, when the male curls his tail after sniffing a female's vagina.

The mountain reedbuck is not a seasonal breeder but the tendency for this species to be severely stressed at the end of the dry season strongly influences the annual pattern of breeding success. At Kekopey ranch, there appears to be an ill-defined birth peak between March and May and observations from eastern Uganda suggest a similar peak. Males show interest in females throughout the year and this species used foreleg striking, or *laufs Schlag*, during courtship; one female was heard to whistle repeatedly after copulation. Irby (1976a) has determined that females are polyoestrous with a cycle estimated between two and four weeks and they have a post-partum anoestrus of similar length; sexually mature at twelve months, the female normally reaches adult weight at fifteen to twenty months, at which time the third molar erupts and the deciduous dentition is replaced. However, poor condition can delay the first oestrus and influences the intervals between births, which range from nine to fourteen months. Gestation is eight months (236–251 days) so that the maximum annual reproductive rate is 1.25 juveniles per female. Males may be sexually fertile before the age of one year but, as Irby remarked, social exclusion minimises the chances of a yearling contributing to reproduction.

The young weigh over 3 kg at birth, they are poorly coordinated and have a well developed hiding reflex. They lie out for two or three months before joining their mother or the mother's group. A female mountain reedbuck discovered dead on Mt Menengai in early April was found to have died in labour with its dead young half out but wedged with foot over head (J. White, personal communication), a reminder that not all births are easy in wild animals.

The rapid growth of this species has been documented by Irby (1976) who charted the growth curve shown in the margin.

Summarising the natural history of this species, Irby remarked that they have survived where larger, faster, more aggressive species have not, because they are adapted to difficult broken terrain which they know well through permanent residence and where predators are at a disadvantage. A grass diet, although limiting in time of drought, is the commonest plant form



Increase in body length in a female mountain reedbuck raised in Loskop Dam Reserve (after Irby, 1976).

within reach and, where the habitat is consistently favourable, their territorial organization is compressible enough to allow local concentrations to maintain themselves. However, smaller, isolated populations are by the same token in continuous danger of extinction because of an incapacity to escape climatic or other local vicissitudes and because of their very limited ability to disperse or recolonize lost ground.





**Bohor
Reedbuck
(*Redunca
redunca*)**

**Family
Order**

Bovidae
Artiodactyla

Local names

Forhi, Tohe (Kiswahili), Nhohe (Kisagara), Bongwe (Kikuyu), Ekal (Ateso), Ebure (Karamojong), Enjaza (Luganda, Runyoro), Abori (Lwo), Esaate, Oweli (Masai), Ebibiya (Runyankole), Arurri (Lugbara), Ngiraguket (Kipsigi), Irukutiet (Sebei), Baroufa (Galla).

**Measurements
head and body**

100—130 cm

height

75—89 cm males

69—76 cm females

tail

18—20 cm

weight

43—55.2 kg males

36—45 kg females

horns

20—41 cm

Note: R. r. cottoni
averages several kg
heavier than

R. c. wardi with horns
averaging 6 cm longer
and 16 cm wider
apart at their tips.

Bohor Reedbuck (*Redunca redunca*)

Races

Redunca redunca wardi Eastern Africa
(Synonyms *ugandae*, *tohi*)

Redunca redunca cottoni Northern Uganda
(Synonym *donaldsoni*)

The bohor reedbuck is well matched in colour with the dry grasses and reeds of its habitat. The forelegs are strongly marked, particularly in the male, which has forwardly hooked horns. The larger, longer-horned *R. r. cottoni* is a form adapted to the flood plains of the Nile Sudd region. This species belongs to the northern savanna zone but it extends as far south as Ufipa and the Rovuma River in the woodland zone of Tanzania, overlapping its range with that of *Redunca arundinum*. In this area both species have been seen side by side in several localities, but the general tendency is for *R. redunca* to be dominant in the more extensive areas of flood plains and reed beds and other open inundated grasslands, while *R. arundinum* is dominant in the uplands and in the smaller glades and valleys that web the *miombo* woodlands. A significant dimension of these habitat preferences is that *R. arundinum* is mainly drought-limited and tends to gather around water in the dry season. Because its distribution follows drainage lines the number of animals drawing together tends to be relatively small but such aggregations include males forced off their territories by drought and these come into contact with other adult males in a similar situation. Much the same pattern obtains in those places where *R. redunca* populations are disrupted by fire and drought or attracted off parched areas on to localized dry season flushes but these concentrations are often bigger than in *R. arundinum* because catchment areas are larger.

In common with other *Redunca* species the bohor reedbuck is ultimately water-dependent (Oboussier and Tyszk, 1964) but it is peculiarly well-adapted to cope with extreme contrasts in flood and drought, in the height and quality of its food supply, grass, and also to extremes in physical exposure after the annual fires that sweep their habitat.

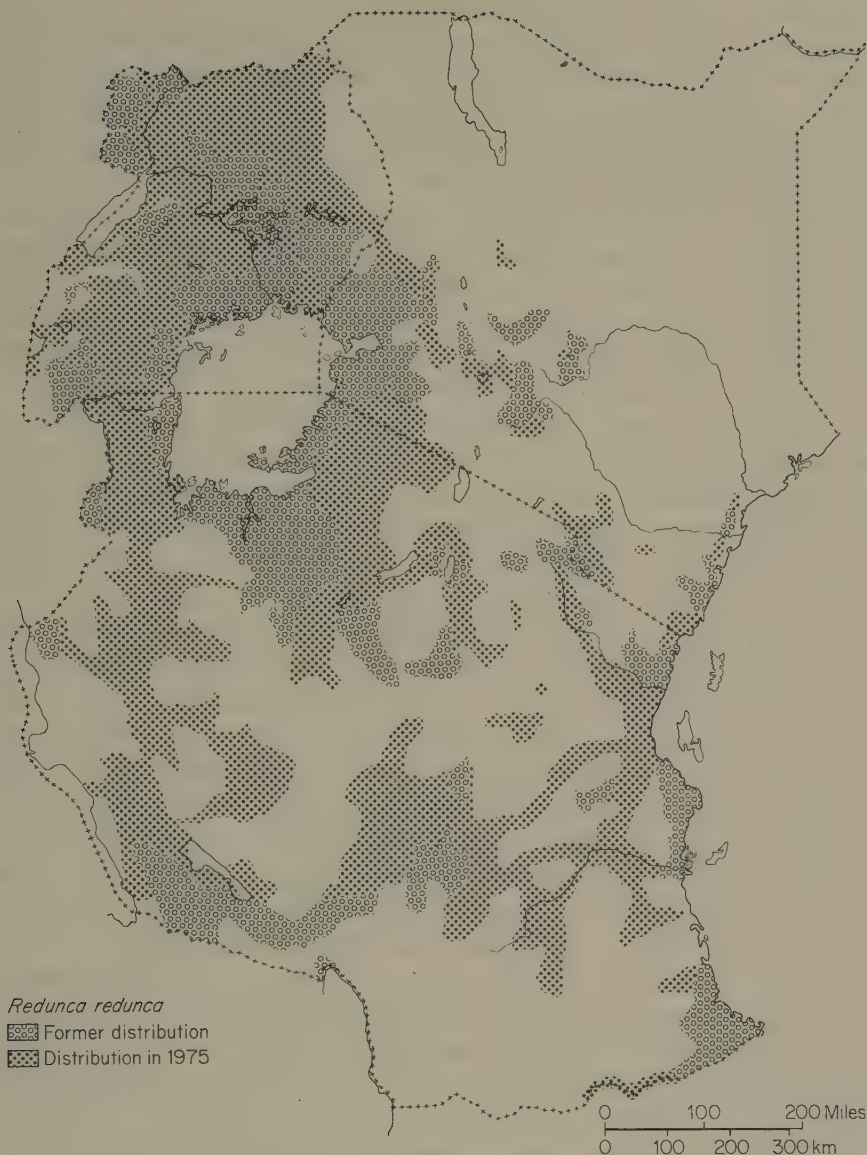
At night bohor reedbuck will typically emerge from thick vegetation and grass along the edges of burns, sometimes joining other open country grazers such as hartebeest, topi, kob or puku. In some farming areas in Kenya they commonly graze at night on young growing wheat and other cereals.

Field (1970) recorded food preferences of two tame reedbuck in the Ruwenzori Park. They fed readily within stands of tall grass and showed a preference for *Hyparrhenia filipendula*, *Sporobolus consimilis*, *Heteropogon contortus* and *Themeda triandra*. In the Rukwa Valley, which marks the



Total range of
Redunca redunca





boundary of the species' range to the south-west, Vesey-FitzGerald (1967) has recorded them as most numerous in the *Echinochloa-Cynodon-Cyperus* community on the main flood plains, grazing on the short grass lawns and sheltering in the long grass. Along the water channels it favours *Vossia* and *Leersia* and it joins topi and puku in concentrating on trampled *Vossia* towards the end of the dry season, cropping the fresh shoots as they appear. Likewise they graze on *Imperata* in the higher burnt pastures. During the period of dry-season fires reedbuck often take refuge in the meander channels which escape the burning.

Percival (1928) recorded them walking long distances at night to raid rice paddies and he pointed out their ability to push through dense elephant grass. He also recorded them as dispensing with water while they can graze off fresh grass, but described them as "shaders" avoiding exposure at midday. Notwithstanding this, I have observed reedbuck sheltering in the

feeble shade of *Acacia drepanolobium* and burnt out cane-brakes on dry open plains 25 km from the nearest water. In this connexion it is interesting that, compared with Uganda kob and bushbuck, the reedbuck's capacity for losing heat through evaporation is very poor and it scarcely sweats at all. Shoen (1971) thought that the reedbucks' inefficient cooling might be partly explained by the fact that the hairs over the whole body have towards their bases a thick greasy deposit which might act as a seal against water loss as well as providing insulation against radiant heat. Shoen's experimental animal was a young male and in males the sebaceous secretion appears to be more copious than in the female. Insulatory and hermetic functions might therefore be added to the possible role of the sebaceous glands but an important context is probably socio-sexual.

A short-term profile of the social system of bohor reedbuck in the Serengeti National Park has been outlined by Hendrichs (1975b). For the period of observation each adult female lived in a home range of 15–40 hectares and their movements overlapped extensively with those of other females. Female offspring were thought to establish their own home ranges gradually and the area of overlap with the mother to decrease slowly. One to five females lived within a single male's mating territory, which was estimated to be 25–60 hectares in extent. Areas shared by females living within different male territories were much narrower than those of females in the same territory. It is not land but access to females that a male defends and Hendrichs observed bachelor parties join a male within his territory. Only when females appeared did the male make a demonstration or chase the bachelors away. Territorial males expel their male offspring while the horns are still mere spikes and these juvenile males join others in bachelor areas sandwiched in between the mating territories.

The reedbuck in Serengeti maintained a stable spatial pattern during the ten days of Hendrich's intensive observation, but Schaller (1972a) saw 35 reedbuck in the same park attracted to a patch of green grass. Such aggregations are probably in response to a very ephemeral resource and so are transient, but there is evidence for very much more sustained groupings and higher densities (Holsworth, 1972).

In the Kidepo National Park as many as 23 reedbuck have been seen together but subgroups could be recognized, each accompanied by an adult male. In this area aggregations are only observed in the dry season between January and April, at which time they are a regular occurrence. Females frequently gather in groups of eight to twelve and they are generally accompanied by subadults of both sexes and one male. In Kidepo the dry season leads to a fragmentation of cover into isolated patches of grass and bush. Many of these are tenanted by single males or by pairs. Further north, where the Kidepo River flows into the vast Pibor flood plains I have seen a focus of many hundreds of reedbuck in March. They were scattered in groups, mostly numbering two to six over less than 30 sq. km of the flat and entirely treeless Kung Kung Valley. In the heat of the day they were resting, often very close together, in patches of burnt-out cane-brake, which provided the only but very scanty shade. Each of these groups was well spaced out from its neighbours but was within seeing distance of up to fifteen other groups. The great majority were made up of male/female pairs

or females with one male and occasional juveniles. At least one bachelor group, numbering 19, was seen.

Down the whole length of the valley a fresh green flush was growing out of the late-burnt stubble on which many thousands of white-eared kob as well as many zebra, hartebeest and tiang were grazing. Throughout this area reedbuck were scattered about but there was a recognizable focus where these were the dominant species and I estimated a density of well over 50 animals per sq. km. Around this centre the density fell off fairly steeply but westwards across more than 200 km of dry open plain an odd reedbuck could be seen from the air almost continuously. Even out on these featureless plains reedbuck invariably run in a tight circle when disturbed, implying some attachment to one spot.

Subsequently a systematic aerial survey of the western portion of the Pibor Plains (at the end of the dry season of 1981) revealed local densities of up to 110 reedbuck per sq. km in the Kung Kung Valley (Frixell, 1980). The Pibor flood plain is dominated by *Hyparrhenia*, a grass that provides superabundant food for herbivores during those periods when the grass is not deeply flooded or so thoroughly burnt off that neither food nor shelter is available. It is the seasonal convergence of reedbuck into more favourable localities (generally on the margin of the flood plain) that explain the very high densities of reedbuck in the Kung Kung Valley and along the entire eastern boundaries of the plains.

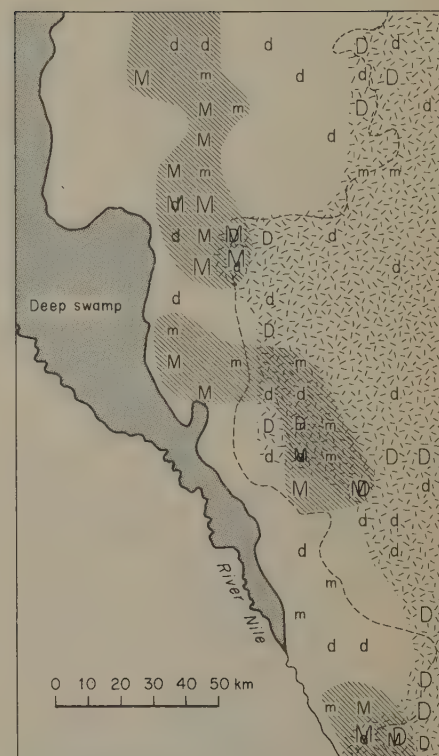
Both vegetation and topography become more varied along the levees and "Duk ridge" which lie between the plains and the Nile. Ground and aerial surveys have shown that reedbuck concentrate all along this western margin in a relatively narrow north-south belt for the worst period of the dry season and that they disperse eastwards into the *Hyparrhenia* with the arrival of the rains. This pattern of dispersal is modified however along the narrowest section of the levee, between Mongalla and Bor, where the reedbuck move nearer to the Nile as the habitat dries out but remain abundant throughout the year, numbers in excess of 63 per sq. km having been recorded late in the wet season, a time when ecological conditions should have allowed maximal dispersion.

Early in the dry season I traversed favourable sections of this levee and, in the area of greater density, counted 23 animals along a 1.5 km transect. There were eight groups, each comprised of up to four females and their offspring and each centred on a separate male which sheltered in a separate thicket.

This reedbuck population is especially interesting because it has probably been compressed over great periods of time and, as floods and drought exert their most lasting influence along the levee, reedbuck here have had to accommodate their social organization and reproductive behaviour to such compression.

Sustained high density seems to correlate with peculiarly long horns. Gemmeiza, a hunting ground at the narrow centre of the Nile levee, has long been known to trophy hunters for exceptionally long, wide-horned reedbuck (see various editions of Rowland Wards records of big game, i.e. Best *et al.*, 1962 and Molloy in Mackenzie, 1954).

It may not be altogether fanciful to characterize the densely aggregated



Seasonal distribution of *Redunca redunca* in an area east of the Nile, South Sudan

□ Dd. December ▨ Mm. March

Dotted line separates *Hyparrhenia* to the east and *Oryza* communities to the west.

Gemmeiza reedbuck as a major genetic focus for a more extensive population. Distribution of the long, splay-horned *R. r. cottoni* broadly coincides with the Nile Sudd ecosystem but it is significant that the major characteristics of this race are more pronounced at Gemmeiza than anywhere else in the Sudd. The average splay of the horns (measured from tip to tip) in the top eleven trophies recorded from the Gemmeiza-Mongalla area is 36 cm with a range of 19 to 67 cm, (the length is only marginally longer). The average splay in the top eleven trophies of *R. r. cottoni* from other parts of the Sudan is 30 cm with a range of 13.5 to 43 cm.

If an increase in the catching surfaces of the horns has a correlation with more frequent contests between males, then the high density at Gemmeiza should favour this development there more than in areas with fewer or more widely spaced males. Gemmeiza is actually the very localized extreme of a process that is widespread in the Sudd and can also be observed on other flood plains. The trend towards larger weapons may not be entirely favourable and there is some evidence that too wide a splay opens defenses to a narrow-horned opponent. A solitary male, whose 38-cm long horns were 52 cm apart at their tips, was collected 200 km north of Gemmeiza within sight of a shorter-horned male with a much narrower splay. The latter was accompanied by two females while the wide-horned animal was solitary and severely scarred all over the head, ears and upper neck. The splay in this individual was probably so wide as to hinder effective fighting, but could less extreme mismatching slow the diffusion of a horn type even if it was marginally superior in its place of origin? Is the selective pressure favouring long splayed horns dependent on exceptional densities sustained over long periods of time? Has this horn type diffused out over the millenia from a focus of higher density? Are longer horns an unnecessary encumbrance at very low densities? Investigation of these questions in the context of a single living species might assist our understanding of the interacting roles of environment, population density, body and horn size and social behaviour in bovid evolution. The Gemmeiza reedbuck population should be studied before it disappears.

Reedbuck concentrations evoke some very peculiar behaviour patterns. For example, Vesey-FitzGerald (1967) observed a gathering of about 100 bohor reedbuck, predominantly males, on the open floor of the Rukwa Valley. Interspersed among adult males, which were standing or lying around, were females, and leaping around with stiff vertical jumps on rigid legs and flashing tails were a number of younger males. Now and then one would stop and lie down in the grass panting but new recruits kept joining the display. Some of the young males appeared to be closely attached to females, presumably their mothers. The females were strictly spectators but Vesey-FitzGerald described all the animals as being so absorbed in the performance that he was able to approach quite closely.

The normally dispersed pattern of reedbuck territories in Rukwa meant that these animals must have been drawn together from a very extensive area. The young males would normally have had to evade or appease a succession of territorial males and their display was the translation into the open of an appeasement device which normally operates in long grass and



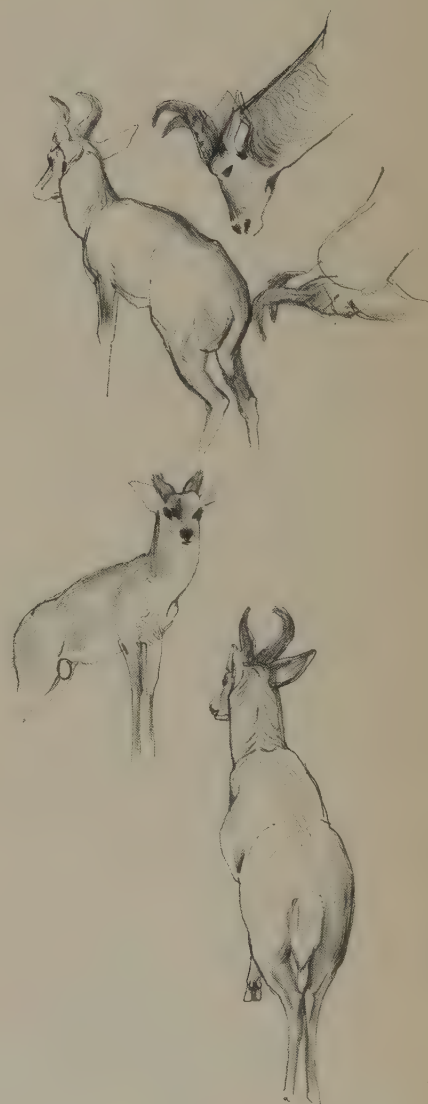
at night. The picture could have had the added complication of sexual behaviour (see p. 339).

Detailed examination of this ritualized leaping, which Vesey-FitzGerald likened to ballet dancing, might have revealed whether it was directed primarily at old adults or the younger males, or whether the behaviour contained more than one element; but the leaps undoubtedly contained information that was directed at the other males and was the product of their peculiarly dense aggregation.

Whistling and bounding are two most conspicuous features of the bohor reedbuck's behaviour. Apart from the obvious purpose of carrying an animal away from an unknown disturbance, it is often assumed that the bounds merely allow a reedbuck to identify an intruder. In fact, a reedbuck usually investigates a disturbance standing still and the sight of a predator often evokes a crouch, freezing or even a skulking creep into thick cover. In any interaction between animals there is the primary problem of identifying the sex and status of individuals and the leap and whistle are probably the mechanisms by which reedbuck recognize one another. There are, therefore, differences in the amplitude, length, style of leaps and in the pitch and number of whistles. Reedbuck have had to invest the leap with an information content that animals in more open habitats can display in slower, less ambiguous postures. For example, for many mammals an elevated rump or "presenting" gesture is a common submission display. This is so for young reedbuck too, but I believe this is carried over into a particular style of leap, which is designed to dampen aggressive responses from neighbours. After rousing reedbuck pairs in long grass, I have sometimes noticed that the adult male may run without whistling or making flamboyant rocking-horse jumps, whereas subadults or females more frequently do both. It could be argued that the male is heavier or less alarmed and it is true that old males sometimes behave with a phlegmatic confidence that is not evident in younger classes.

In some areas gatherings are restricted to the hours of darkness. Along the margins of the Mayanja swamp in Buganda, pastoralists burn off the reedbuck's prime habitat during the dry season, creating corridors of open lawn between the papyrus and scattered patches of thicket and unburnt reeds on higher ground. During the night reedbuck converge on these lawns with a fairly dense spacing of perhaps 100 m or less between individuals, to much whistling and bouncing. It is impossible to know from how extensive an area such nocturnal concentrations are drawn; but up to midnight and before dawn the night is punctuated by a chorus of whistles as the animals emerge from their daytime retreats to graze. Answering whistles come from every direction and a torch reveals a larger number of animals than could have been suspected were present in the vicinity on the evidence of daylight observations.

One difficulty for the observer is that the bohor reedbuck is primarily a nocturnal animal and may feed at some distance from its refuge. Tracking a reedbuck that was raiding crops, Percival (1928) followed it to a habitual shelter 8 km away and he thought this was not an unusual night's activity and remarked that he had chased one with horse and hounds for over 14 km.



In many habitats attempts at estimating density are complicated by seasonal movements, by nocturnal and cryptic behaviour and poor visibility. My own dry season estimates along the Narus Valley in Kidepo and in Singo county suggest that at least one pair can be encountered about every half kilometre along a suitably reedy valley. This estimate can be compared with the crude yardstick of some hunting records of the Uganda tse-tse division. During the Ankole-Masaka tse-tse clearance scheme a total of 6,630 bohor reedbuck were shot by professional hunters in an area of 3,000 sq. km. This enclosed about 1,000 linear km of drainage lines that were suitable habitat for reedbuck. The reedbuck continued to reproduce and a few survived the extermination campaign but the figure of about five animals per kilometre of valley bottom appears to be a realistic estimate.

Very little information exists on mortality but dry season hunting with dogs and nets takes considerable numbers in parts of Uganda.

The dominant predators vary with the region. In Serengeti, Schaller (1972a) thought that the reedbuck population was kept depressed by leopards; the ranges of both species being restricted to a narrow belt that follows the watercourse. Percival (1928) referred to reedbuck lying up near lions, and Schaller observed one keeping quite still for three hours while it lay six metres away from a pride of lionesses. He also watched an adult escape the lion's attention by crouching, a common subterfuge by reedbuck and one frequently directed at humans.

Because the young are kept well hidden for at least two months after birth, records of breeding are scarce. Schaller mentions small reedbuck being seen in Serengeti in September and April and there are Uganda records for April and November. Very young animals are scarcely ever seen at the height of the drought and I have not seen any on the Pibor plains in March. Grass fires could destroy or expose many young, but dry season heat stress may be an even more important factor in selection for seasonal breeding.

Two free-ranging females that lived on Kikagati island apparently betrayed their oestrus period by the activity of the gland beneath the ear (T. Nuti, personal communication). The male's interest and copulation coincided with the exudation of greasy secretion from this gland. As females live within a male's territory they are likely to be discovered very quickly, but the odour of the secretion wafted through the air and brushed off on the grass would certainly help males to detect and track down females. When a Kikagati female was in oestrus the male would sometimes make a sound like a toy trumpet and would rush round her in a circle making high jumps. This sound was quite different from the whistle and was not heard in any other context. However, the behaviour was not seen to lead on directly to copulation. Considering their extensive area of overlap without interbreeding the observed differences in the courtship patterns of this species and *R. arundinum* are of great interest.

The male holds his ears back and head down with the nose raised as he approaches the female and he mounts standing very erect after sampling the female's urine and curling his lip.

Gestation is said to be seven-and-a-half months and the young hide themselves, changing the place of their retreat each day. After a mother

has finished suckling her young the breaking off of contact may be difficult. I have watched what appeared to be a game of tag between a mother and her offspring, as the infant pursued its mother round and round a large termite mound. The mother suddenly detached herself and the young one disappeared into the grass. I was uncertain as to whether the termite mound acted as a contact-breaking device but the performance certainly gave that impression.

Young reedbucks are quite often found by the Bahima herdsmen in Ankole and Buganda. They sometimes rear them with a nanny-goat foster mother and I have seen a subadult being herded with the sheep and goats.

Captives have lived ten years.





**Southern
Reedbuck**
(*Redunca
arundinum*)

**Family
Order**

Bovidae
Artiodactyla

Southern Reedbuck (*Redunca arundinum*)

Local names

Tohe ya kusini (Kiswahili), Suwela (Kinyakyusa), Ngholigata (Kihehe).

Measurements head and body

134–167 cm

height

84–96.5 cm

tail

26–27 cm

weight

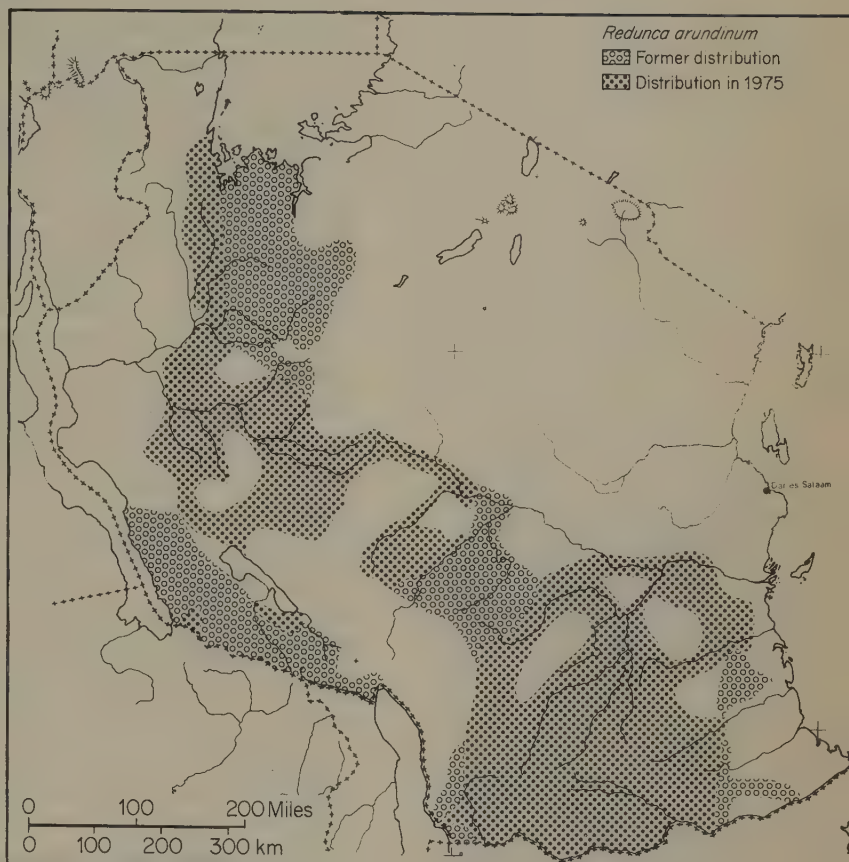
68 (51–80) kg males

48 (39–64.5) kg females

horns

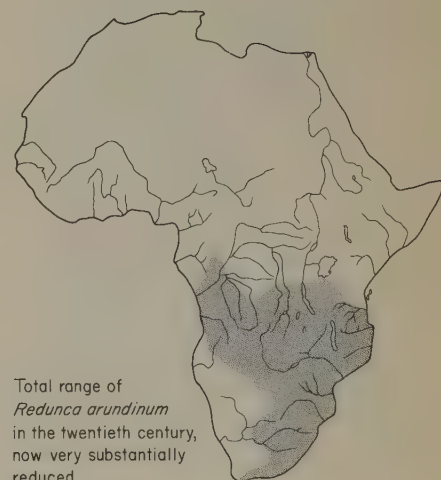
30–45 cm

Note: The Southern Highlands of Tanzania are sparsely inhabited by this species. Records of *R. fulvorufula* on the Kitulo Plateau (Rodgers in Sale, 1977) need confirmation.



Largest of all the reedbuck, with horns that sometimes approximate to those of a waterbuck in shape, the southern reedbuck is rather variable in its colouring. Some males are a dark brown while others are a light buff colour like *Redunca redunca*. It has not been investigated to what extent variation is genetic, sexual or influenced by age or climatic factors. The glandular spot beneath the ear seems to be poorly developed in some populations. The males have a very characteristic pale zone at the base of the horn. The black and white markings of the forelegs are also very noticeable.

Originally found very widely throughout the moister areas of the southern savannas, this species occupies habitats that are typical of both the other reedbuck species and its distribution suggests that it might have replaced *R. fulvorufula* in some highland areas. On the other hand it seems to be inferior to *R. redunca* in more open habitats. For instance, *R. arundinum* is very rare in the Rukwa Valley where *R. redunca* is extremely common (Vesey-FitzGerald, 1964), but the former species is again common along the seasonally flooded valleys feeding into the Ugalla-Malagarasi river system. They are also widely distributed in the rank grassy valleys and glades within the *Brachystegia* woodlands. The end of *Miombo* woodland marks their northern limits and the greater part of their range is contained



Total range of *Redunca arundinum* in the twentieth century, now very substantially reduced

within this huge vegetation belt. In Zululand Venter (1979) found that although they visited valley bottom grasslands for grazing, particularly after burns, the animals showed a much stronger overall preference for short and fairly open shrubland. The species seems best adapted to a delicately balanced mosaic of scrub and grass. The antipathy of this species for dense thicket growth has been discussed by Deane (1966), who noted a dramatic decline in reedbuck as thicket replaced *Themeda* grasslands in Zululand.

The southern reedbuck has been studied in South Africa by Jungius (1971a, b) and Venter (1979). The favourite food grasses, which are often the dominant species in their habitat, include *Leersia*, *Panicum maximum*, *Hyparrhenia*, reeds and sedges. There is no evidence, however, that it is a specialized or very selective grazer; rather that it is able to live and feed within a tall grass mosaic that surrounds waterlogged valleys and is under-used by other herbivores. It sticks, whenever it can, to vegetation that is no shorter than itself. Like *R. redunca*, these reedbuck will keep quite still or even stay lying prone when their neighbourhood is disturbed and only leap up when they are approached to within about ten metres. They utter a wheezing whistle, which resembles that of *R. redunca* but may be a bit louder. Sometimes there is a popping sound which coincides with their leaps up over grass. Jungius has described this sound being produced twice as the hindlegs jerk backwards and outwards at the peak of each leap. This noise seems to result from a release of air from the inguinal pockets that lie in the groin. Since the glands produce scent, the high jumps may very well leave an aerial scent trail behind. The whistle is very commonly linked with the high bouncing jumps that are typical of all three reedbuck species.

Although reedbuck probably do leave a scent trail, the whistle has undoubtedly become its principal advertisement of presence and it is used in almost any situation where there is a change in the animal's position vis-a-vis its neighbours. The main stimulus for the whistle is movement in the animal's immediate vicinity. Jungius (1971a) frequently saw males in their territories or at their watering pools whistle when another animal (even of a different species) was near or came into view. He also saw a female beside a waterhole whistle after a second female had retreated from her. Another female kept on whistling (over 50 times) until she had thoroughly investigated an unidentified movement in the grass. Whistles are also made when the animal itself is moving or about to move and Jungius very frequently noted animals whistle and make advertising jumps in the vicinity of waterholes. They did this whether other reedbuck were present or not, and very often just before moving off. Pools are likely meeting places for reedbuck, particularly during the dry season, but animals meeting are likely to be outside their home ranges. Thus when two males meet at a waterhole their meeting generally ends with a typical bovid display in the proud posture followed by an unhurried retreat by one or both animals. However, it seems that whistling and pronking tend to precede and follow the "proud" display and that both actions serve as long-distance spacing mechanisms. Because the whistle seems to play no part in the preliminaries to fighting it is tempting to see it as conciliatory in effect. Jungius described sequences where animals answered each other. A pair approached a waterhole at which a solitary male was grazing. When the grazing animal was seen by the new

arrival it elicited a display. Looking up, the other male also displayed and then turned to groom its flank. The new arrival whistled, at which the other replied. The newcomer then jumped in self-advertisement; the other responded with a display before moving slowly away.

The mainly nocturnal activity of the southern reedbuck is modified by conditions, particularly during the height of the dry season, when water must also be visited. At this time Jungius saw the Kruger Park reedbuck progressively extend their activity more and more into the morning and begin earlier in the evening; he never saw them seek shade. During the wet season they rest longer, graze less and ignore the rain, although Jungius noticed them stay in cover if it was windy. He estimated that an average of seven daylight hours were spent resting, three ruminating and three grazing. When they are resting they prefer areas with a good all-round visibility and will often lie on the leached slopes of a termite mound.

Females are generally more wary but Jungius twice saw a resident female chase off the female of an intruding pair while the two males were fighting. Butting is not uncommonly resorted to, and a female rejecting copulation may kick out as she turns away.

Social structure is loose and, like other reduncines, strongly influenced by density. On richly vegetated coastland in Zululand, Venter recorded a density of about 16.6 reedbuck per sq. km. Home ranges averaged five or six hectares and there were extensive overlaps in male and female ranges. Ranking determined male relationships and once dominance hierarchies had been established they only changed as a result of severe fighting. Nonetheless groups in excess of three were rare and only accounted for 10% of all sightings; the largest group numbered thirteen.

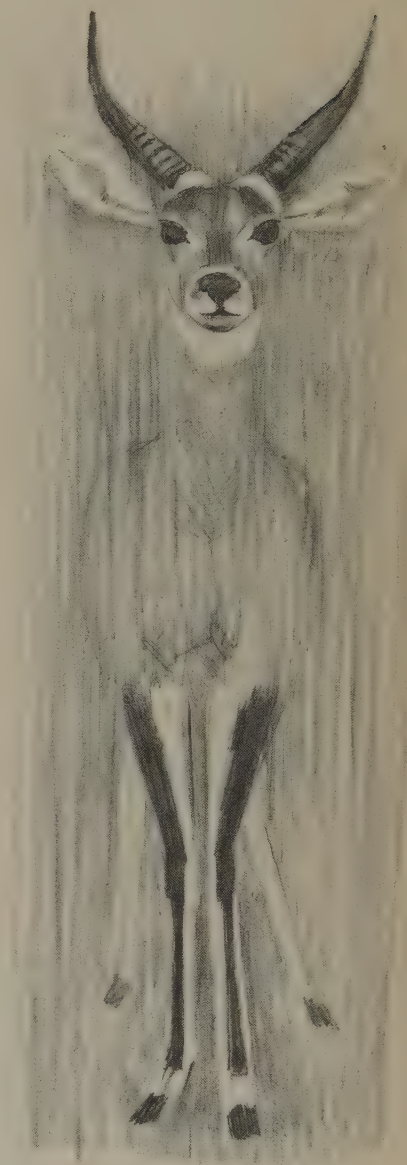
In the Transvaal, where reedbuck were ten times as sparse, Jungius found a very different situation with each male spaced out in a defended territory which was shared with a resident female. Joint movements were always initiated by the female, which led her young and/or a male in single file. This was particularly noticeable when going to water. Males never coerce their females, although they may chase them away from an approaching adversary in an encounter. Sometimes a male may actively seek a female out:

"a male rests 200 metres away from a grazing female. They cannot see each other... the male gets up, grooms himself, looks around, whistles twice and pronks twice. The female interrupts grazing, faces in the ram's direction, whistles twice and continues feeding. Upon this the male walks straight towards her." (Jungius 1971a)

A male has also been seen to track its mate down by scent.

Mating and the rearing of the young occur within the home range, but there is minimal contact between the pair for the period immediately preceding and following the birth of the young.

It is not known how stable the pair associations are. Fires and drought in the dry season expose the reedbuck and force them to find cover and water at some distance from their home ranges or, if they are better placed than their neighbours, they have to adjust to an influx of other families. Concentrations form in the dry season, excluded from the remaining reed-



beds and other patches of suitable habitat by the established territory holders and harassed by constant activity in the immediate vicinity of a waterhole. Jungius described the refugees concentrating on uncontested and, for the reedbuck, unfavourable open ground some 800 m from the water. The size of refugee groups tends to be limited by the incompatibility of adult males to a maximum of about seven, but reedbuck are decidedly more social in the dry season. Solitary animals are frequent in the wet season but this is unusual during the dry.

Territories around permanent water contract in the dry season. Jungius found one that was 35 hectares in the dry season became 60 hectares in the rains and, as competition for living space rose, he noted other pressures on territory holders. A male would permit females and young to join his family group but drove off adult males. But even in this case a very persistent second male was seen to join one family for two months in spite of continuous fighting with the resident male. That new territories can be propagated through sheer persistence was shown when a three- to four-year-old bachelor edged in on one of two well-established territories that Jungius had been studying. Eventually the original owner's aggressive responses waned and it ceased to visit the newcomer's area.

Typical territories extend 300—500 m along rivers and reach up valley slopes until they peter out in bush. Within the territory the animals' centre of activity tends to change with the seasons.

Territorial displays between males include a slow and deliberate defaecation, which appears to be a powerful stimulus for the rival and leads to either an immediate attack or the retreat of the inferior male. Dung is normally dropped at random but Jungius once found a place corresponding to the stamping ground of other species. The area comprised an arena of trampled grass with faeces and urine dropped in the centre; it was used for one month and was visited by the same male at regular intervals.

Territorial encounters followed a similar pattern to those of other ungulates in that proud postures are interspersed with head flagging at close quarters, which leads on to tilting of the horns forward or sideways. If horns are lowered there is invariably a clash with both participants lunging forward simultaneously and clashing their horns noisily together. The horns of this species are quite long and sharp and fights account for well over a third of all male deaths in the high density Zululand population (Venter, 1979). These occurred mainly in competition for oestrous females.

The principal enemy of the southern reedbuck over most of its range is probably the leopard, which shares its habitat, but in some areas the cheetah is also important. Records of kills in the Kruger Park show that cheetahs favour reedbuck very highly as prey, but there are more reedbuck killed by leopard as this is a commoner and more widespread predator. The number of reedbuck killed by wild dogs and cheetahs rises dramatically during the dry season when they are more conspicuous and their defensive strategies are less effective. Pythons and smaller carnivores, such as serval cats and jackals, are probably a danger to the newborn.

Breeding occurs throughout the year but there is a birth peak in South Africa between December and May.

In courtship the male investigates the female's genitalia, whereupon the

Numbers of reedbuck killed in the Kruger Park. (Preference rating: kill frequency relative to abundance.) Data from Pienaar, 1969; Jungius, 1971.

Predator	Numbers of reedbuck killed	Preference rating
Leopard	124	2.2
Cheetah	60	5.2
Hunting dog	36	1.35
Lion	35	0.27
Crocodile	3	
Hyaena	2 (under-represented)	
Python	1	
Baboon	1	

female lifts her tail and urinates. Leg kicking is rare. After sampling the urine over his nose and performing *flehmen*, the male may then proceed to mount if the female does not leap away. The single copulatory thrust is accomplished while the female's flanks are very tightly clasped. After dismounting, he may rub or lick the female's neck. No chasing was seen by Jungius but he reported a widespread belief that the peculiar popping noise that is made by the inguinal glands in both sexes occurs during courtship behaviour and he described an incident that is suggestive of a submission displayed by a female towards a male. This female suddenly started to run around a male at high speed with her body stretched out and neck extended. Then, raising her head, she threw her rump up exaggeratedly and made the noise. At times the leaps were interspersed with long floating bounds covering some metres. The whole sequence of galloping, popping and jumping was repeated until the female finally came to rest beside the watching male.

Gestation has been stated to be seven or seven-and-a-half months. The female segregates herself some weeks before giving birth and drives off her young of the previous season. After the birth the young, which weighs about 4.5 kg, hides itself and only emerges for the mother's single midday visit which lasts 10 to 30 minutes, of which suckling occupies two-and-a-half to four-and-a-half minutes. At least one nocturnal suckling is likely and the young one generally changes its hiding place after each visit. Concealment is maintained for up to two months and after a further two months both mother and young emerge and may join the male.

Young animals have mock chases or fights in which they feint, throwing the forequarters to the left then to the right, like a playing dog. The lowering of the forequarters with the haunches raised seems to be a submissive posture, most frequently adopted by an inferior or young animal to superior males, and Jungius observed that animals adopting this position are not attacked. The posture is very commonly seen as a female or young animal approaches a male to sniff noses. A resting female approached by a male often sniffs, nods her head and then lays her head on the ground.

Horns first appear in males at about the age of six months. When the young male leaves the company of its mother it may associate with the male but bachelor herds have not been seen and Jungius suggested that a young male probably seeks to establish a territory for itself at about three years of age.

Kob
(Kobus kob)

Family

Bovidae

Order

Artiodactyla

Local names

Ensumu, Empala (Luganda), Emparaki
(Runyoro), Til (Lwo), Etil (Ateso),
Hamraye (Arabic).



Kob

(*Kobus kob*)

Measurements head and body

160—180 cm

height

90—100 cm males

82—92 cm females

tail

10—15 cm

weight

94 (85—121) kg males

63 (60—77) kg females

horns

40—69 cm

Races

Kobus kob thomasi

Uganda (formerly Lake Victoria littoral)

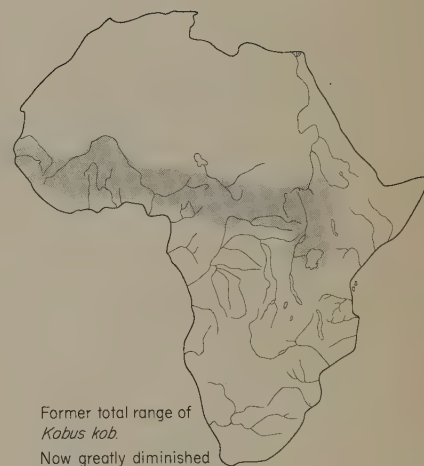
Kobus kob leucotis

Kidepo and Kiman valleys, Lamwo
(vagrant)

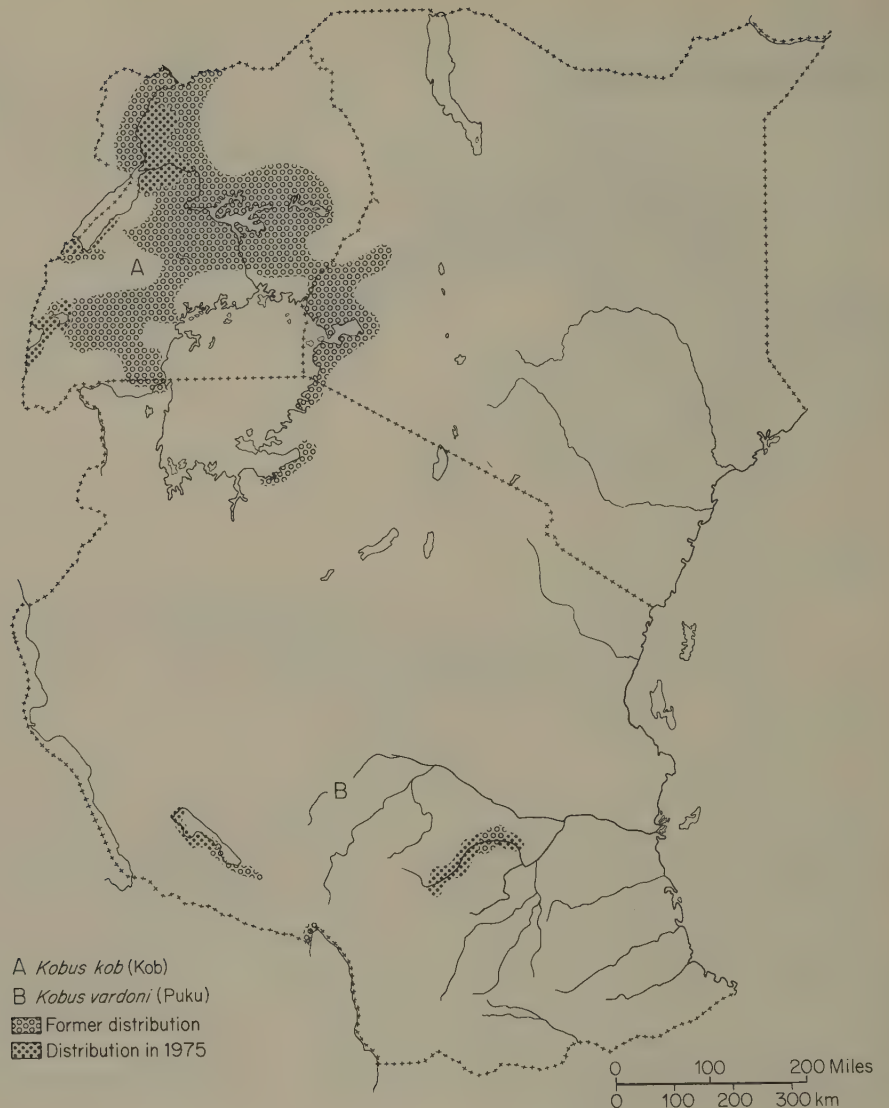
The male kob is a robustly built antelope with muscular neck and thick lyrate horns. The female is much more slender and hornless (although aberrant females with thin twisted horns are known). The usual colouring is rich cinnamon rufous with white underside and throat chevron and black markings on the legs. In Acholi, males are rather variable, some having dark patches and others almost black coats. In this area the rufous Uganda populations come into contact with the black *K. k. leucotis* of the southern Sudan, isolated individuals or small groups of which sometimes wander into northern Uganda.

The kob was once very much more widely distributed than it is today. At the present time there is a scattering of populations across western and northern Uganda. They require low-lying flats or gently rolling country close to permanent water, without severe seasonal extremes and such highly favoured localities are today being taken over for agriculture or ranching.

Short grass grazers, particularly those in the lower size ranges, generally depend upon a larger ungulate community that will ensure that the conditions they need are available throughout the year (see Vol. I, pp. 38—41). It is very likely that the kob originally evolved to take advantage of overgrazed conditions in the vicinity of lakes and rivers. If the kob's ancestors had habits at all resembling those of the reedbuck, it is likely that they initially took advantage of the extensive areas of closely cropped grass created by hippopotamus, buffalo and other large ungulates grazing within a few kilometres of water. Once they had appropriated this niche they might have been capable of extending their range further into fire-climax grasslands, the importance of which has greatly increased with the rise of man's



Former total range of
Kobus kob.
Now greatly diminished



influence. When kob are numerous enough they can keep down limited areas of sward through their own numbers.

Considering the riparian origins of the reduncines and the kob's proven physiological need for water (Shoen, 1971), it is clear that any extension of ecological range out into drier habitats must stop short of the point where the population is robbed of access to moist green growth or adequate water. Evolving within the rich habitats surrounding lakes and rivers, reliance on water or moist food is a built-in factor that puts a limit upon the expansion of populations and favours the kob's attachment to a locality.

Today kob are closely associated with several larger animals over the greater part of their range; the most significant species from the point of view of grazing maintenance are hippopotamus, topi, hartebeest, buffalo and cattle. Fire also plays an important part over most of the kob's con-

temporary range. Under conditions of drought very large concentrations can also gather in low-lying localities where the water table is higher and green grass is available.

Bindernagel (1968) studying a population of exceptionally high density found kob played a large part in maintaining their own pasture, although they shared their habitat with some buffalo, hartebeest, oribi and warthog.

Bindernagel recorded the most heavily grazed grasses in the kob concentration areas as two *Hyparrhenia* species, *Brachiaria brizantha*, *Setaria sphacelata* and *Paspalum* species. Other important grasses are *Andropogon gayanus*, *Chloris gayana*, *Echinochloa* and *Digitaria*. In common with most other ungulates, bitter aromatic species such as *Cymbopogon* are avoided. Field (1970) observed the food habits of a tame kob in the Ruwenzori Park and listed *Panicum repens*, *Sporobolus pyramidalis* and *Chloris gayana* as dry season preferences and *Cenchrus* for the rains, a choice that emphasizes the kob's habit of feeding from a short sward.

If kob are assumed to have evolved from a type of reedbuck, their major innovation is the ability to congregate and move, *en masse*, from one resource to another. Such movements generally follow seasonal changes in pasture up and down the catena but, in areas of extensive flooding, journeys can involve many hundreds of kilometres. Daily treks to water in the dry season may also require a walk of 10 km or more.

In spite of their emancipation kob retain a reduncine attachment to particular localities and follow daily and annual patterns of movement that suggest the existence of strong local traditions. The same grazing grounds and watering places are returned to day after day or season after season. Although ritualized scent marking is absent, excretions and body scents may play an important role in their orientation.

Reedbuck territories are spaced at densities that will support breeding pairs throughout the year. Kob can maintain an even territorial spacing comparable with that of the reedbuck only if the entire population is dispersed through a rich and homogenous pasture. This only occurs in some populations and for limited periods of time. In such circumstances a balance between male and female distributions at the time of breeding can be achieved by a close synchronization of the breeding cycle with an appropriate period in the population's annual cycle of movement. Since the timing of reproduction is determined by a combination of factors (such as survival rate of the young and nutrition of the mother), such synchrony is only achieved where environmental pressures converge in favour of a clearly defined breeding season, as they do in South-eastern Sudan.

In the absence of such a synchronization seasonal abandonment of territories and frequent aggregation and movement by the females decreases the chances that they can be inseminated within a region of stable territories. Therefore, unless the more usual reduncine pattern of male territories is closely synchronized with the female kob's reproductive cycle it is unable to perform one of its primary functions: to ensure that all females are mated.

It is therefore very interesting to find that in those areas where breeding takes place throughout the year, populations are dense and greater ecological diversity makes wholesale migrations between distant ranges unnecessary, the territories appear to be very uneven in size and density.



The subject of how males come to be distributed in territories that range from 200 sq. m to 0.5 sq. km has provoked a large body of research because of its bearing on the biological function of territory. The observations and conclusions of some of the researchers have been widely at variance, partly because of real difference between regions, partly because interpretations on inadequate data have acquired an over-elaborated theoretical superstructure.

Molloy (1957) writing of kob in the southern Sudan described solitary males in territories of several thousand square metres which they held throughout the day. He recognized that females and immature animals formed independent groups. Buechner (1961a) first described dense foci of small territories that occur within limited areas in the Semliki (Toro) Game Reserve and he likened these territorial grounds to the mating arenas of certain birds, borrowing the term "lek" to describe them. Buechner (1974) observed that most oestrous females converged on only three or four of the 30–40 territories that are concentrated together. Some of the males on the clustered territories monopolize copulation and oestrous females appear to be drawn in towards this centre from more peripheral areas for the purpose of mating.

Spinage (1969a) saw no evidence for the conclusion that the dense aggregations ensure a maximum rate and efficiency of reproduction and he was sceptical about the idea of a complete reversal of behaviour in which the female seeks the male, instead of vice-versa. In other localities and outside the territorial grounds, kob males can be seen to detain females that pass through relatively large territories and copulate successfully (see Bourlière and Verschuren, 1960).

Leuthold (1966b) pointed out that this broader territorial network also existed in Semliki and suggested that the spacing of territories grew progressively denser around these aggregations. Leuthold (1966) estimated that two-thirds of the territorial males in the Semliki, which has a density of 45–50 kob per sq. km, were generally dispersed over the surrounding country.

Bindernagel (1968) working in Achwa, an area with the highest local density of kob yet recorded, (61 per sq. km) plotted four grounds, each of which had a high density of small territories. More dispersed territories were also observed throughout the kob's range. Bindernagel emphasized that there were numerous mixed groups in Achwa.

In the Ruwenzori National Park, Modha (1973) found only 4.5% of male territories were clustered on territorial grounds. This area has a density of 3–18 kob per sq. km and he pointed out that there was a positive correlation between population density and the size of territorial grounds. He was the first to draw attention to the possible role of pheromones on territorial grounds, noting olfactory behaviour in males on newly acquired territories. He postulated that an accretion of female urine odour may attract females to particular points as well as males.

Individual kob have no lasting links with other individuals but females are gregarious and form herds of 30–50 (with a range from two to many

Frixell (1980) has recorded densities of one thousand per sq. km near water during a drought.



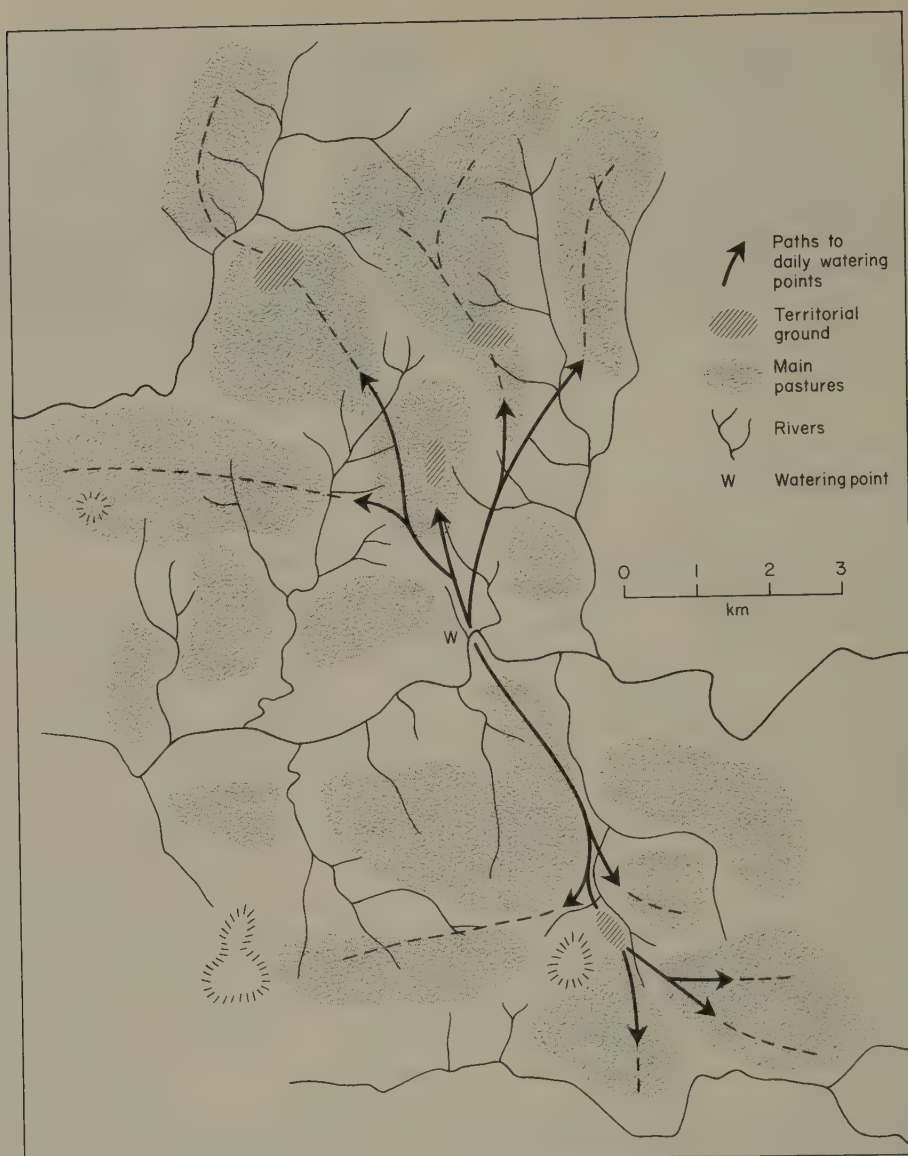
thousands). The females also initiate most movements and are significantly more mobile and more social than those territorial males that remain attached to their static territories for as long as possible.

It is also the females that respond directly to seasonal changes with wholesale migration and it is the females that lead the daily movement to water. Whether these movements are long- or short-term, large- or small-scale, they are usually exceptionally predictable as to timing and route.

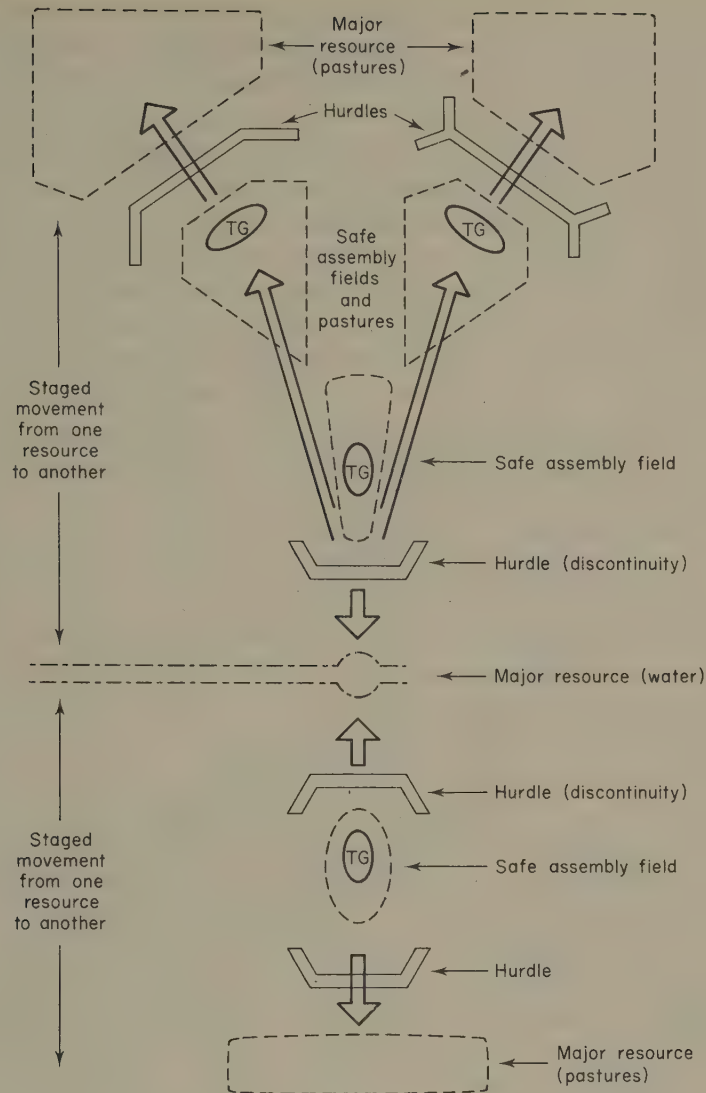
For the individual animal a routine is acquired from the mother but the higher the density of animals the more females will take their cues from other females.

Males also follow the females and may be an integral part of their herds for variable periods of time. In the high density Achwa herds the proportion of males ranged from 12% (in two herds of more than 100 animals) to 34% of herds in the 10–19 size range (Bindernagel, 1968). All-male herds of several hundred animals may also associate with the females especially during dry-season marches. Bindernagel recorded kob from a radius of 12 km following well-trodden traditional pathways during the dry season to visit a particular watering spot, moving as a body to do so. At dawn each morning virtually all these kob were drinking at a particular point along the Adawa River; shortly after daybreak they began to depart for the long trek back to their grazing areas. Such observations illustrate the kob's tendency to establish traditional routines and imply the existence of discreet population units. In the same locality as Bindernagel's study, Brooks (1957) recorded a mob of 700 kob being chased several kilometres away from their normal grazing areas by a pack of wild dogs: they fled as a consolidated mass. After the dogs had made their kill, the kob divided up into two groups, one consisting mainly of females and young, the other of yearlings, but within three hours all the kob were back where they started. Both Bindernagel and Brooks thought that a subpopulation's attachment was to a grazing area.

Leuthold (1966b) proved that kob have an intense attachment to a locality by experimentally removing some territorial males up to 22 km away where he released them. Six out of eight eventually found their way back to their original piece of ground. Leuthold also recorded marked females again and again within a small locality. All-male aggregations numbering from 46–600 individuals likewise remained in a favourite locality.



Bindernagel mapped out the normal grazing limits of the Achwa population (above) and he traced the pathways by which the kob travelled to their single traditional watering place, which was the same for kobs from both banks, (crossing sides was thought to be very rare). The position of the territorial grounds within this network of paths and pastures seems to be specifically related to "staging" during the regular movement of animals from one resource to another (opposite). In Achwa and the Ruwenzori Park I have noticed a tendency for kob to check their movements and collect in the vicinity of territorial grounds. While the grounds themselves may exert an attraction there are also environmental and behavioural influences that could delay movement and cause kob from a wide catchment area to collect in assembly fields. I watched small groups of kob moving down the Nyamagasani Valley in Ruwenzori Park during 1960 and 1962 and I was struck how they emerged near the crater rim of Lake Katwe, where there



is a sudden steep drop. The kob would remain grazing on these heights for variable periods of time before they descended into the crater to drink and return. Close to the rim there was a territorial ground. This site shared with the Achwa territorial grounds the characteristics of being on a slight slope near a vantage point with good visibility, the grass was short and all grounds were established alongside or very near an established route and close to a discontinuity in the topography, in the Katwe case an abrupt one.

What delays the kob's progress probably varies from place to place. A positive factor may be the attraction of a feeding spell along the journey. An open site with good short grass and the presence of kob drawn in from other pastures would help improve security. A small environmental change along the way ahead could also induce a pause in progress. Larger changes involving the prospect of a descent into thicker vegetation or a rocky gully might induce longer pauses and still bigger aggregations before the kob finally risk possible ambushes by predators. Most sites are grazing grounds

in their own right and there are usually some non-territorial males in the immediate vicinity which are more or less residential. Too little is known about the spatial and temporal distribution of population sub-units to know whether some of the females close to the territorial ground are less than transient, but Buechner (1974) recorded 50% of mature males remaining almost permanently within 500 m of a territorial ground, whereas only 14% of the female population remained in the area. Their numbers are certainly augmented by kob from further afield and male numbers may be swollen by bachelors that first accompany the female herds and then remain. This may explain how bachelor herds of 500–600 can assemble close to the territorial ground. Raised areas readily become islands of occupation during the wet season, at which time kob may leave lower-lying areas because the grass is growing too fast and too coarse. On the better drained areas large numbers can concentrate without churning up the soil and they can, by heavy cropping, keep the growing grass at their favourite stage until the end of the wet season. To the proposition that territorial grounds are a product of high density there is the additional link with localized movements by significantly large population units. To this can be added Leuthold's (1966b) observation that the clusters might have become traditional centres of orientation for local population units. Another correlation is that the kob's reproductive cycles are not sharply seasonal in the areas where territorial grounds occur.

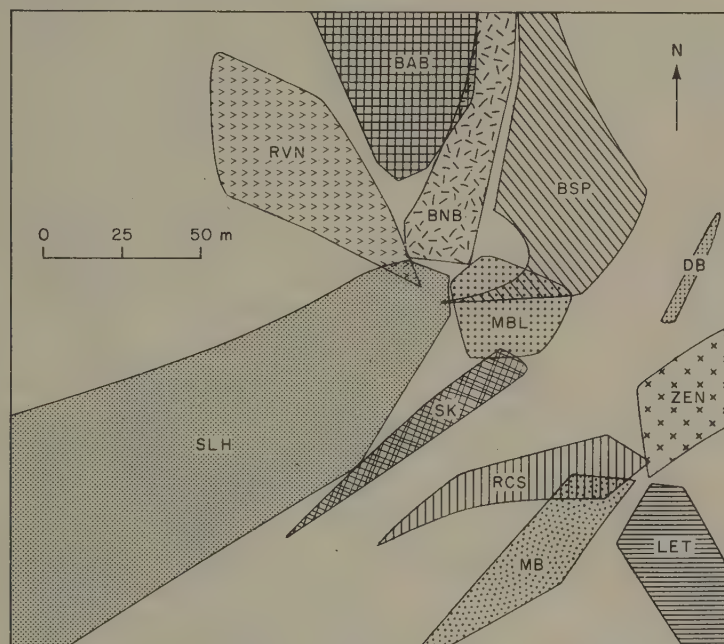
I have already argued that the conventional territorial system can function reliably only if mating is synchronized with an even dispersal of both sexes in a suitable environment. The attachment of males to mobile female groups becomes especially significant if the females come into oestrus at unpredictable times. Their condition excites intense interest in all mature males but copulation is impossible while groups are on the move. As soon as movement stops, all males are likely to compete for the females and in a high density population this would be attended by intense fighting and disorder. At this juncture two points should be remembered. One, that all the large populations in East Africa have built up very recently from more modest ones. Second, that a reduncine attachment to routine and to place has established traditions in every kob population and introduced an element of predictability into the life of an individual kob, thus the origins of a contemporary routine may be of many years establishment. At low population levels, oestrous females can be inspected, produce urine, be courted and inseminated by a male with a conventional territory or, in his absence, by a male transient.

The actual formation and development of a territorial ground has never been studied but nearby sites that are identical to assembly fields in all but their strategical siting have conventional territories, so it is likely that continuous traffic and an accumulation of sexually active males must eventually make the normal system untenable. Nonetheless a normal territory or territories might be a necessary precursor for the formation of a territorial ground.

An oestrous female escapes being the direct focus for male competition by entering a territory and her attraction towards dominant males may be strongly influenced by the protection he offers, directly or indirectly,

from harassment by lower-ranking males. In a featureless landscape the sanctuary offered to a travelling oestrous female by a territory may be signalled by the presence and the behaviour of a dominant male, but in a crowd of mature and sexually active males the female is faced with the problem of identifying her refuge.

For any olfactory mammal scents are the commonest guides to behaviour and, as Modha (1973) suggested, the most likely signal is the smell of urine dropped by previous females while they were being tested by territorial males. A long tradition, comprising a complex of experiences, may lie behind the female's firm progress to one or more highly localized points, but the beacon leading them with such exactitude is likely to be a massive scent signal to which they themselves contribute.



"Functional centre" of Katwe territorial ground, Ruwenzori National Park. Areas of movement for 12 territorial kob for the period 24–29 July 1971: redrawn from Floody and Arnold (1975) rendering "perimetres of movement" as blocks to reveal radial patterns around two foci.

Without identifying the olfactory stimulus, Floody and Arnold (1975) were able to locate very accurately what they called "functional centres" on the Lake Katwe territorial ground mentioned earlier. These centres consisted of two focal points where a variety of female and male activities took place including copulation and aggression. This study suggested that it was the focal point and not the individual males that attracted the females, which subsequently mated with a succession of males after their arrival at one or other of the two foci. Seven males converged on the major vortex while four or five males clumped around the second. Although males defended all the boundaries of their elongated territories, the most intense activity occurred only at the end closest to the vortex. The perimeters of each male's movements showed that most territories radiated out like slices of a circular pie (above). There are very frequent and intense fights as other males constantly attempt to reach the central points: as a result there is a rapid turnover of males controlling access to the foci, with tenancies of one or two days in contrast to normal territory holdings of one or more years (Leuthold, 1966b).



Floody and Arnold documented the fortunes of several of these temporary tenants, which commonly followed a transition from less to greater activity, a brief spell at the centre, then an exit from the scene. One particularly active and dominant male began his 26 day career on the territorial ground by defending a more peripheral territory and then displaced another male in a territory at least 200 m long. This animal defended the extensive boundaries around his hinterland but all his matings were concentrated close to the vortex showing that, although he was equally available to females in other points of his first and second territories, they neither chose him nor did they respond directly to his "quality" until he was in control of a central section of the territorial ground.

Graduated intensity in the agonistic behaviour in male kob around a territorial ground has been remarked upon by Leuthold (1966b), who correlated it with a graduation in territory sizes. Such a behavioural gradient may be of less significance in relation to inferior territorial status than it is to changing hormone levels in males from the nearby bachelor herd. This is both a source of recruits and a refuge for the exhausted. The environs of a bachelor herd are a likely scene for the transition to territorial status. In several species of antelopes it is common to see intense rivalry among bachelors as they mature and the herd may be the setting at one and the same time for a transition from immaturity to a fully adult role and for refugee ex-territorials; in some species bachelors form strictly linear hierarchies.

As with most ungulates the younger kob males fight most. Out of 68 fights observed by Leuthold, both partners were adult males in only three cases and in 43 of them both contestants were subadult or immature. Although the youngest adults are not normally tolerated in the territorial clusters, Leuthold noted frequent interchanges between the bachelor herd that is associated with each cluster. In a comparison between the age composition of the clustered males on the ground and those on the dispersed single territories he found a very similar age structure. Of the younger animals that were fully mature Leuthold found 22 on the ground and 19 occupying single territories, of the elder classes he found 13 on the ground and 16 on single territories, the oldest males were only found on single territories. For the latter class the threat display is generally adequate to keep the territory intact. A slow deliberate walk is adopted with the ears strongly depressed, the head up and the tail raised—the penis may have erections and is a very conspicuous organ in the kob's displays. The head may be lowered as if to fight and then abruptly raised again. Head flagging while standing in a confronting position is common. If very excited there may be a clash of horns and, if this develops into a fight, the contestants try to throw one another off balance with much twisting and butting. The impact of horns is heavy and kob are sometimes killed in these duels.

The animals on territorial grounds do not behave like true territory holders in a number of respects. They exert little influence on a female's movements. Mating with several males takes place in areas within a few metres of a boundary. The distribution of a male's activities within his defended area is crowded closer to the single focus than it is to other boundaries and the shape of territories as shown by Floody and Arnold reflects this orientation. The brevity of tenure may be partly due to the

intensity of competition and to physical exhaustion, but there is a disproportionate ratio of fights within the immediate orbit of the vortex in comparison with those involving conventional perimeter defence. This implies that the animals are fighting to get to a particular thing more than they are attempting to extend space around themselves. This is less competition over a boundary than a direct confrontation with as many other males as can gain access to the primary source of stimulus. Finally, gradients in the intensity of aggressive behaviour suggest that two unmeasured and possibly interrelated factors may be at work. One is the individual's androgen-testosterone levels. The other is the direct effect of proximity of olfactory stimuli, both from males and females, and their accumulated excretions. This is difficult to assess, although I have watched kob sniffing soil and Modha (1973) reported males violently horning the ground with the phallus partially erect.

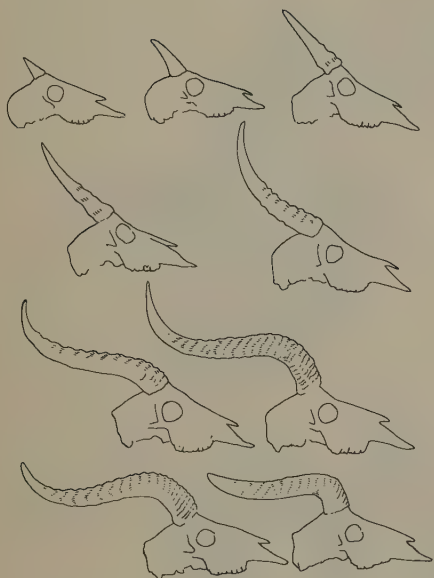
It is quite clear that the clustered territories on the territorial grounds are not mere miniatures of those found elsewhere. They show fundamental differences from conventional territories and I have outlined the factors that I think likely to have influenced their formation. I consider that they are in some respects an artefact of non-seasonal breeding in populations that are relatively mobile at the local level but highly compressed for significant periods of time and at the sites I call assembly fields. The territorial grounds probably enhance reproduction by reducing direct harassment of oestrous females and also ensuring that few of them escape fertilization. They do not involve a female choice of mates, as has been suggested, and they may be founded upon well-established and highly localized traditions.

In this connexion the history of the kob populations in Uganda and eastern Zaire is of some interest. It is known that kob in the Parc National Albert have fluctuated between 15,000 in 1931, 3,000 in 1940 and 5,000 in 1959, extremes that represent densities ranging from 25 to 5 per sq. km. Bourlière and Verschuren (1960) suggested that habitat change (principally fire suppression), competition, predation and disease may all have played a part. Across the Ishasha River in Uganda, kob were thought to have decreased by about half between 1920 and 1930. Further north, domestic and wild ungulates on the Semliki flats had also suffered from rinderpest and trypanosomiasis, and all cattle were evacuated in 1924. By 1935 kob were described as particularly plentiful in this area and the high population level seen today had, by local reports, been reached at about this time. In Achwa there was also a large human population and herds of cattle in the early years of this century. Trypanosomiasis decimated the human population and their stock and there was a total evacuation from Achwa by 1915. Brooks (1961a) writes

"One cannot imagine that game could ever have been abundant in the vicinity of Jonam or Acholi homesteads. Such must have been the situation near Lolim and Belim hills judging from the number of families living there; yet at present in the neighbourhood of these two village sites exists one of the largest concentrations of Uganda kob to be found anywhere in Uganda."

The evacuation created an ecological vacuum which may have taken some time to fill, as wildlife was still reported to be scarce around Achwa in 1935,





(the Semliki kob were well established by this time). However, an astonishing increase was noticed in the whole of this region in 1938.

In the recolonization of habitat, kob, hartebeest, waterbuck and buffalo were the principal species available, of these the kob has the fastest recruitment rate. Densities of kob approaching the present ones were thought to have been reached 40 years ago and the concentrations of territories date back at least as long in Semliki.

In Uganda kob breed throughout the year but breeding is more seasonal in the South Sudan (Kingdon, 1981) and in Senegal (Dupuy, 1969). The males' courtship display is broadly similar to that of other antelopes. The female is approached with the head held low and nose up and the genital area is sniffed, this generally releases urination in the female which is in turn followed by a lip curl by the male. If the female is in oestrus the male becomes excited and he prances, flashing his coloured legs; his neck is arched back and the chin raised, exposing the white throat chevron towards the female. Sometimes the female runs away or may lie down and Dupuy (1969) saw a male rouse such a female with pawing by the forelegs. He may bleat and if she persists in circling to avoid him he may butt or nip her hindquarters. If she stays the male nuzzles her and then he may touch her belly by stiffly raising his foreleg (*laufs Schlag*). Throughout the display he parades with erect penis and finally he may mount and copulate with a single thrust. A unique feature of the kob's courtship display is the male's continued display after copulation. Both partners may whistle after coitus and this may be answered by neighbouring males. The male also shows great interest in the female's hindquarters, pushing his head between the female's thighs and licking the inguinal glands and udder (Buechner and Schloeth, 1965). Leuthold (1966b) suggested that post-coital display might serve to make the territory more attractive to a female. Buechner thought that females might return each year for mating in preferred territories within the territorial cluster but I suspect that their visits are more likely to be dictated by the timing of her oestrus in relation to her routine movements at that time.

An unusual courtship was observed in western Uganda when a kob was seen trying to mount a female waterbuck for about an hour, the waterbuck appeared compliant but the kob was too short in the leg to achieve insertion. However, a kob has bred successfully with a fertile *K. defassa* = *K. megaceros* hybrid in the Khartoum Zoo (Gray, 1954) to produce a *Kobus* with three distinct species in its immediate ancestry.

Gestation is nearly nine months (261–271 days) (Ulmer, 1966). Buechner (1974) determined an average post-partum interval of 40 (21–64) days and he thought practically all adult females were continuously pregnant, with calf or both simultaneously. From the South-eastern Sudan I have put on record the huge annual migrations of kob on the flood plains east of the Nile (Kingdon, 1981). Here the great majority of young are dropped at the end of the rains in about November–December. The rut takes place between the Pibor and Akobo valleys in March and April when most of this seasonal population, numbering nearly one million animals, is collected together. Dupuy (1969) thought that there was a rutting peak in Senegal in the early dry season producing a birth peak in the rains.

During April 1980, when there was drought in the Pibor-Akobo area

densities of well over 1,000 kob per sq. km were recorded near water (Frixell, 1980).

The young are born in patches of longer grass or bush. Here they lie up for a variable period of six to eight weeks being visited by the mother for suckling mainly in the morning and evening. She calls them out with a low bleating call. The older fawns accompany the mother grazing and remain with her for six or seven months. Leuthold (1967) reared a baby kob which was imprinted on him. The parental bond was well illustrated after his seven-month-old animal had joined a herd of wild kob and yet came back to him in response to his customary calls.

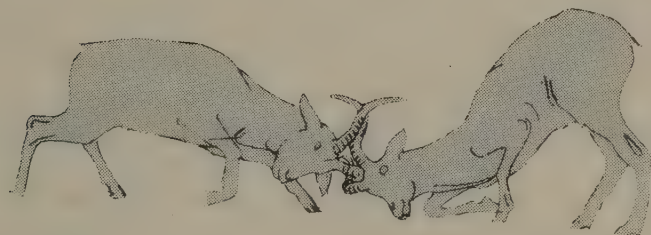
Development of the horns is illustrated opposite.

Like other species living in the open, kob suffer from numerous predators, the chief ones are hyaenas, lions, leopards, cheetahs and hunting dogs. There has been very little study of predation on kob, although they must provide most of the food for predators living near kob concentrations.

The attachment of kob to a locality is so strong that human settlement can proceed with the kob attempting to go on living almost in the new villages, where of course they do not last long. Kob are very vulnerable to hunting dogs, nets, bows and arrows; the young are easily speared. Their survival near settlement is virtually impossible because of the ease with which they can be killed. On the other hand, they respond very well to protection and build up their numbers rapidly. Their potential as a managed resource is very considerable.

Bindernagel showed that ranching and cropping of this species in Achwa was a practical possibility. Subsequently his report drew no response from the authorities and a local politician established his cattle ranch in the area, yet Buechner (1974) has pointed out that in terms of energetics kob have rates of assimilation, respiration and growth that, as far as is known, are higher than any other species of mammal.

The kob, it seems, is one more example of an exceptionally valuable natural resource that is going to waste unless more positive wildlife policies are implemented.





Puku
(Kobus vardoni)

Family
Order

Bovidae
Artiodactyla

Measurements
head and body

126—142 cm

height

77—83 cm

tail

28—32 cm

weight

77 (67—91) kg males

66 (48—78) kg females

horns

40—54 cm

Puku (*Kobus vardoni*)

The puku is slightly shaggier, with rather heavier proportions than the kob and thicker, shorter, less lyrate horns which have less stem than kob. Haltenorth (1963) considered *K. vardoni* to be a race of *K. kob*, but the separation of the two populations is probably of long-standing. Ansell (1968) has treated the two forms as members of a super-species.

Puku populations are found in a wide scatter over central Africa along the margins of lakes, swamps and rivers and on flood plains. They are perhaps more ready than kob to live in small strips of grassy country or even glades within the southern African woodland zone, and the dispersal of populations and the maintenance of gene-flow might have been eased by a tolerance of woodlands. Nonetheless, the species is ecologically restricted and is only found in pockets of suitable country.

Like the kob they respond to seasonal changes by moving up and down the catena. During the rains they live on higher ground but move down to graze the margins of lakes and rivers during the dry season.

Child and Richter (1969) noted strong seasonal changes in the preferred grass species of puku in Botswana. *Brachiaria latifolia* was eaten in quantity between January and March, *Eragrostis* in July—August and December and in the latter month *Vossia* shoots became important, as they do in the Rukwa Valley. In addition, Vesey-FitzGerald (1965) records them feeding on lawns of *Sporobolus*, *Panicum*, *Digitaria*, *Cynodon* and *Chloris*.

Parties of three to 15 females with immature young of both sexes are common. During the dry season these may amalgamate into larger parties numbering about 50 animals. However, densities have never been recorded that approach those of kob. Like kob, males are dispersed in territories and bachelor parties or all-male aggregations have been reported; Verheyen (1951) described these regularly amalgamating with herds of females and young and then separating again for no apparent reason.

Puku breed throughout the year but Verheyen reported that after congregating near water for the dry season the males take up their territories again with the first heavy rains. Soon afterwards small bands of females are seen and Verheyen reports a birth peak nine months later.

Puku probably behave very similarly to kob but de Vos (1965) watching territorial displays was unable to see penial erections, as are usual in kob.

Puku show population fluctuations but the mortality of young is generally very high. Mitchell *et al.* (1965) note their extreme vulnerability away from water attributing this to their being relatively slow and clumsy. Jungius (1971a) described water as being as important a refuge for puku and lechwe as long grass is for the reedbuck.

At one time puku occurred on the plains at the north end of Lake Malawi. Their habitat was taken over for the cultivation of rice and sugar and a similar pattern is occurring in Uganda for the kob.

Some cropping has been attempted in the Rukwa Valley but no observations were published. In view of the remarkable recruitment of the Uganda kob and the probable similarity between kob and puku, the biology of the puku and its economic potential in Tanzania should be investigated.



Former range of
Kobus vardoni



Waterbuck
(Kobus
ellipsiprymnus)

Family

Bovidae

Order

Artiodactyla

Local names

Kuru (Kiswahili), Kuyu (Kipokomo),
Nhulu (Kisagara), Ekhuro (Lubukusu),
Saramet (Masai), Apoli (Lwo), Emosemos
(Karamojong), Ensana (Luganda,
Runyoro), Labi (Lugbara), Ngurames
(Kiliangulu, Saramaitit (Sebei)).

Measurements
head and body

177—235 cm

height

125 (120—136) cm

tail

33—40 cm

weight

240 (200—300) kg males

180 (160—200) kg females

horns

55—99 cm

Waterbuck

Kobus ellipsiprymnus

Groups

ellipsiprymnus group (white crescent round rump) South-East Africa.

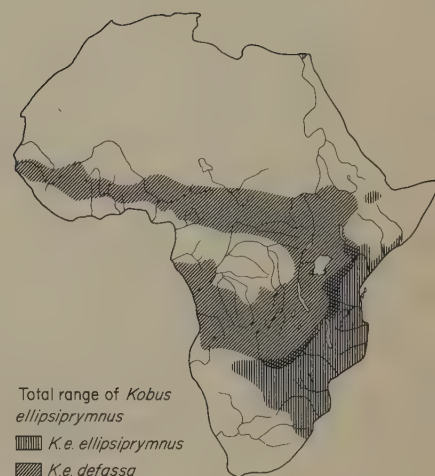
defassa group (white hindquarters below the tail) North-eastern, Central and West Africa.

The waterbuck is a big shaggy animal that is rather variable in colouring, even within a single population, with dark grey and rufous animals occurring in the same herd. In general there is a tendency for the males to be darker and greyer and for the females to be warmer in colour. In addition to the two major types listed above there are regional differences in average body and horn sizes. The *defassa* group have the wider distribution in Africa, and islands of *ellipsiprymnus* well within the range of *defassa* might have been engulfed by relatively recent extensions by populations of the latter group. In the areas of overlap in Kenya and Tanzania a variety of intermediate rump patterns can be seen which are presumably the result of hybridization.

The waterbuck's shaggy coat is heavily impregnated with a smelly, greasy secretion. This might serve two functions; one being the individual scent recognition that seems to be characteristic of all territorial ungulates, the other perhaps being water-proofing in an animal that occasionally enters the water to escape harassment or to browse on inundated pastures.

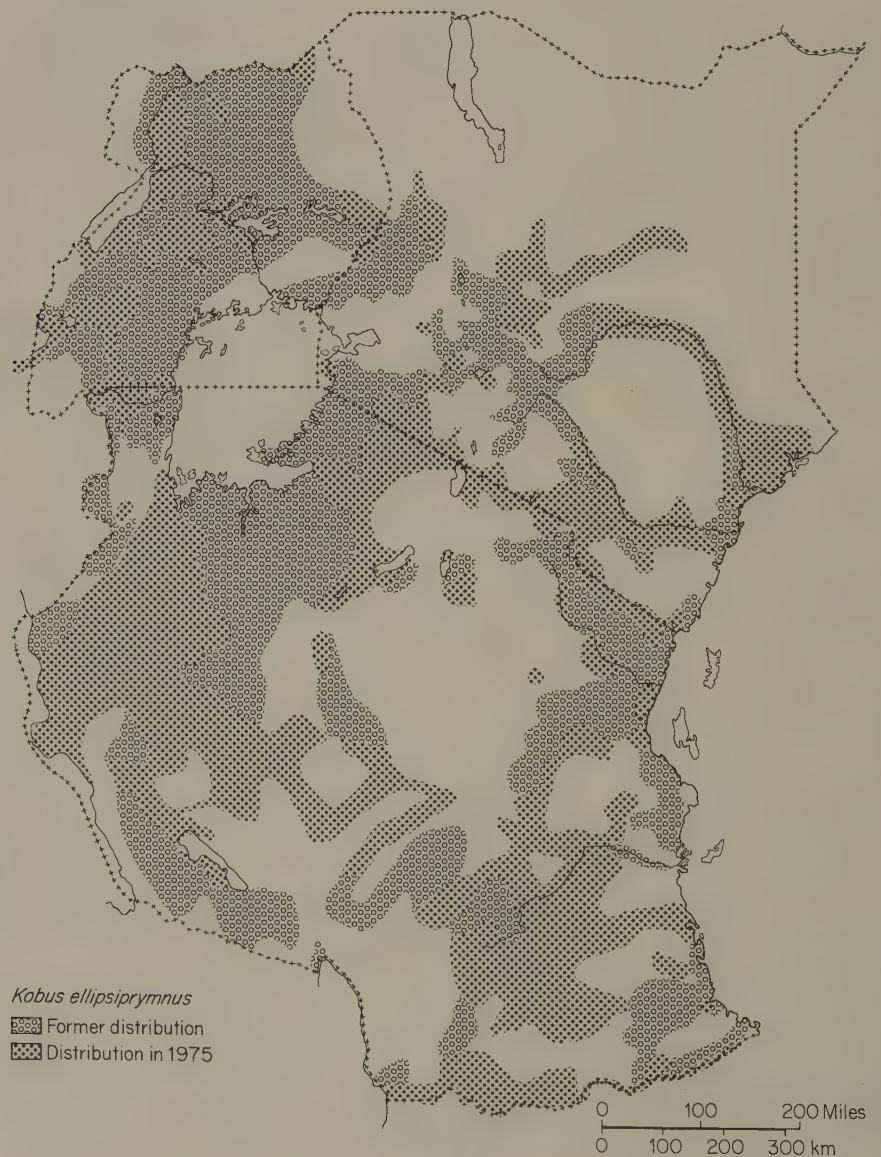
Only male waterbuck normally carry horns and their length is some indication of age. In western Uganda they have exceptionally long horns, reaching their greatest length at about six or seven years, at which time there may be as many as 27 annuli. Animals from other localities have fewer, rather more crowded or indistinct annuli and generally shorter measurements. An aberrant male was shot by Mrs Toni Nuti in western Uganda which had exceptionally heavy, thick horns growing horizontally instead of vertically (see drawing). Females usually have a horn rudiment in the form of a bony lump on the skull and, in rare individuals, a loose curl of horn may be visible. It is interesting that one female in the Ruwenzori Park developed full-length horns but had one of them broken off, possibly in an encounter with a male. If this was so it would illustrate how inappropriate and dangerous it is for a female to have horns in a society that is dominated by very aggressive males for which the horns are presumably the major signal triggering their competitive territorial behaviour.

The waterbuck is a rather sedentary animal dependent on plentiful and fair quality fodder throughout the year in well vegetated country. It requires a fairly mixed diet and feeds on medium and short grasses, reeds and rushes, *Phragmites* and *Typha*, at both early and mature growth stages. They have been recorded browsing on the leaves of *Diplorhynchus con-*



dylocarpon and feeding on *Sclerocarya* fruit and *Acacia* pods. They will graze off erect grass tussocks as well as on the flushes of grass that follow burns. Child and Richter noted a distinct seasonable preference for *Paspalum commersoni* during the Botswana wet season. Other favourite grasses were *Cynodon dactylon* and *Brachiaria latifolia*. In Uganda, *Hyparrhenia filipendula*, *Chloris gayana* and *Cenchrus ciliaris* have been noted, while *Cyperaceae*, *Andropogon*, *Heteropogon*, *Cymbopogon*, *Digitaria*, *Dichrostachys* and *Panicum* species have been observed in Tanzania.

The onset of the rains leads to some wandering, mainly by subadults, and the greatest observed distance travelled by a female marked by Spinage (1969) was 32 km. Once settled, however, waterbuck are relatively sedentary and the males in particular tend to stick scrupulously to their territories. These are not marked by any deliberate means; both dung and urine are dropped at random. The main advertisement of occupation is the male's



actual presence and his scent as he walks about. This is so strong that I was once surprised to discover a party of waterbuck in a patch of woodland purely by smell; their unexpected presence being confirmed by picking up their tracks and flushing them.

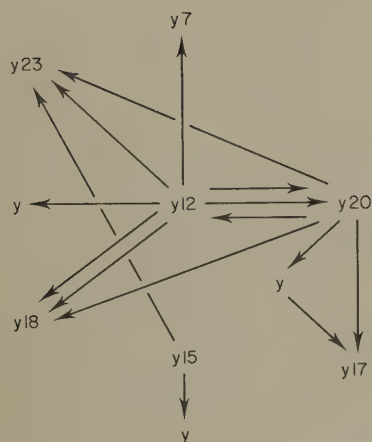
The combined roles of sight and scent in the social life of the waterbuck are well illustrated in Spinage's diary record (1969a) of a male which suddenly broke off investigating a female and started to walk in a straight line staring ahead, whereupon a male stranger about half a kilometre or more away started to run. The first male walked to the spot where the strange male had stood, sniffed around and then proceeded to track him like a dog, holding his nose about a foot or so from the ground, only when he reached the boundary of his territory did he stop.

The mornings and evenings are generally spent grazing (at which the female spends more time than the male), but the most intensive feeding probably takes place at night. Hanks *et al.* (1969) noticed seasonal differences in the pattern of male and female activity in the Kafue Park, Zambia. During the wet season females remained in the thickest country while males grazed the valley flood plain. The same population grazed together during the dry season, spending the day in the open and the night in the thicket and an aggregation of 45 animals was seen to break up into smaller units before nightfall. Such patterns are very likely to be influenced by predation; in areas where they are shot at during the day they keep to thickets and only emerge on grassland by night.

Much time is spent ruminating and resting. Indeed, waterbuck appear very phlegmatic, an impression enhanced by their heavy gait and quiet demeanour. They are generally silent but for a snort of alarm and the female has a soft modified snort and penetrating bleat that is directed at the young. Fighting males occasionally utter a bleating snort call when excited and a wounded animal will sometimes give a bellow of distress, as will a harassed juvenile.

The life of an individual waterbuck has well-defined phases. The calf is left on its own for about three weeks, after which it stays with its mother in a loose association of other mothers and calves. Calves come together as soon as they are old enough to leave their retreats and these associations may continue after the nine months of semi-dependence on the mother, either in a break-away "bachelor" or a more temporary "spinster" group. Kiley Worthington (1965) speculated that mother-daughter associations might continue throughout their lives but Spinage did not find females forming permanent social bonds with any sex or age class. Where there is a juvenile wandering phase this is essentially the product of surplus population, it is readily absorbed if there are unused or recently vacated areas in the vicinity. Thus the frequency of wanderers will tend to increase with higher density populations. Wandering males join up with a bachelor herd before they are one year old. Unlike some ungulates, these bachelors do not normally include elderly individuals but only young males of pre-territorial status. Bachelor herds have their own hierarchies that are roughly based on age, as they tend to remain in the same group for about five years. A structural model of the bachelor herd has emerged through Spinage's (1969a) observations:



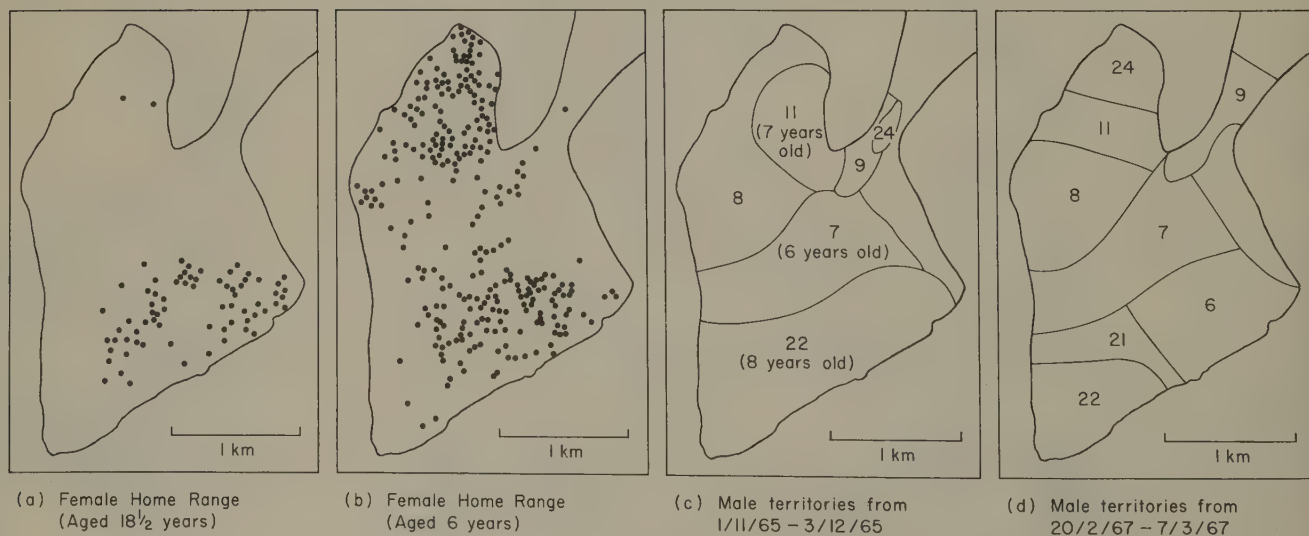


Typical sequence of sparring contacts between bachelor waterbuck (from Spinage, 1969).

"The mean herd size of seven animals may be related to the age at which the male takes up a territory, the inference being that two animals of the same age do not tolerate one another. Herds are thus composed of, say, two animals in their first year, in which antagonism will not be developed, and an average of one animal per year class thereafter up to the age of six."

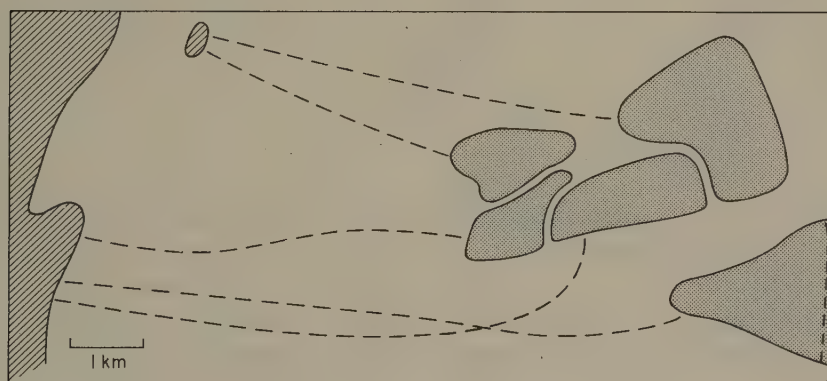
When opportunities to form exclusive territories arise, the older, more dominant individuals become more attached to their land and less attached to the herd. Hanks *et al.* (1969) saw a herd of bachelors inherit a territory after its owner was killed by a lion. After some months a dominant member of the group started chasing the others and in about a month had established himself in the area with no substantial change in the former territorial boundaries.

Spinage illustrated the dominance hierarchy of a typical bachelor herd with a diagram of sparring sequences (see margin). The bachelors generally range over the territories of several solitary adult males, where they are normally tolerated. Likewise adult females have fairly extensive home ranges which tend to contract with advancing age. Here again Spinage has given a detailed picture of the influence of sex and age in waterbuck society through his observations at Mweya; a typical female ranged all over the 450 hectares of the peninsula and adjacent area, while an aged female restricted her movements to one corner (see below). Females become attached to areas rather than to males, so that males with the best and largest territories tend to be visited by more females for longer periods. Although the male tries to dissuade them from leaving his area, these attempts are never successful and females on the move do not generally precipitate conflict between neighbouring males. A female moves about as an individual and has a home range that overlaps several male territories although the resources of the area, its topography and, perhaps, factors in the waterbuck's individual histories may lead to the coincidence of several female home ranges.



Waterbuck home ranges and territories on Mweya Peninsula (after Spinage, 1969.)

Sightings of the movements of a single female on the Mweya peninsula (below, opposite) were typical of several others. It is interesting to compare their use of this area with that of the territorial males. Spinage studied the peninsula shortly after the hippo and most of the hyaena populations had been shot out, as a result of which cover regenerated and grazing improved, hyaenas had also ceased to be such a hazard and these artificially contrived factors probably assisted the steady increase in waterbuck population that Spinage recorded. On the basis of continual observation he was able to draw the boundaries between territories with considerable accuracy and the patterns of changing ownership are perhaps best appreciated in a comparison of how the peninsula was divided into six territories in December 1965, as against eight territories in March 1967, when the same owners were redeployed together with two others—one of which was a returned absentee. Another interesting detail was that y9, which had originally owned most of y7's territory, often tried to return but was chased off. The dynamics of these changes over three years were explained in detail by Spinage (1969a, b, c). The choicest territories are not necessarily won by the biggest animals and both Spinage and Herbert (1972) noticed extreme timidity in two particularly large males. Ageing animals probably tend to lose out to younger males after four or five years, although a single male in the Parc National Albert was believed to have occupied the same area from 1931 to 1939. The size of territories appears to be partly related to dominance and the preferred areas have a good water frontage, but there are areas where high density forces the males to use the water front as a neutral zone and aggressive behaviour is reserved for a hinterland of particularly small territories (see below).



Waterbuck territories (stipple) in relation to the lake shore and watering points (hatching) at Kanyanja, Ruwenzori National Park (from Spinage, 1969).

As with most antelopes, readiness to fight is in inverse proportion to age and young males can be seen sparring together much more frequently than older males. Established territorial males tend to respect one another's boundaries and limit their displays to brief exhibitions of the "proud" posture. The full display in more exaggerated form is seen in subdominant animals: the lateral view is presented to the opponent with the neck arched, the tail is held out and the penis may be erect. The animals may circle or parade back and forth and the subdominant may attack bushes or horn the ground. I have seen a male fray the tip of one of his horns in an onslaught



on stony ground immediately after being chased by a territorial bull at Kidepo. If the display brings the animals into a frontal position and they touch noses, this is almost invariably followed by a butting contest. When the animals are excited this becomes an impressive performance, with each animal parrying any attempt to get in a thrust to the side. Deaths are not uncommon, particularly in areas of high density and hence of great competition. Walther (in Grzimek, 1972) described what appears to be a rare form of contest, (possibly noted in a zoo): "They may also stand like a team of horses beside each other and grapple with each other with hooked horns to test their strength. When the opponents are of unequal strength, the weaker changes to this method where the stronger one may not use his full body weight." Spinage saw young males as most prone to fighting and this was usually precipitated by their invasion of an established territory. However, any incursion by a male into another's ground will lead to a fight. Notwithstanding the sometimes lethal results of fighting, territories are a very effective spacer of male waterbuck along their littoral habitats.

The hornless females are seldom aggressive but Herbert (1972) saw a female try to bite another female that was drinking, and mild butting is not unusual in female groups.

The tendency for waterbuck populations to have a littoral distribution along the margins of rivers, valleys and lakes makes meaningful estimates of the density rather difficult. Spinage arrived at a mean of 5.5 (0.4—23.3) per sq. mile for the optimum habitats of the Ruwenzori Park and Lamprey (1963) gave 6.8 per sq. mile for transect areas in Tarangire. For less favourable habitats estimates range from 1.3 on the Mara (Fraser-Darling, 1960a) to 1.9 in the Nairobi National Park (Foster and Kearney, 1967).

The largest limiting factor on waterbuck populations is predation, principally on the calves. The local abundance of the predator species will influence the rate at which waterbuck are killed, but hyaenas, leopards and lions are probably the most important.

Spinage estimated a 50% loss of calves in their first year of life, and as these were often abrupt disappearances, the most likely cause was hyaenas. Because hyaenas leave no remains, an assessment of their role is almost impossible to measure but Bere considered that prior to the removal of the hyaenas most of the waterbuck calves on the Mweya peninsula were eliminated at or soon after birth. There were about 20 hyaenas at that time and close grazing by the hippos allowed very little cover in which to hide the calves.

In the Kruger Park, where detailed records of kills have been kept for many years and where waterbuck are fairly common, hyaenas killed 19 waterbuck in a total of 125 recorded kills (Pienaar, 1969a). Although the sample is small, this is a very high proportion considering the relative abundance of the waterbuck (1.75% of the total prey species) and it suggests that waterbuck are particularly vulnerable to hyaenas. In this area crocodiles may be even more important predators with 21 waterbuck of a total of 125 observed kills. Lions also kill an unbalanced proportion of waterbuck in the Kruger Park (10.59% of all kills) and it is interesting that they were apparently unselective as to sex, particularly as several authors have invoked lions to explain the waterbuck's sex ratio, which is generally in the region of two males to three females. The Kruger figures for other predators are also interesting when the age classes are compared.

WATERBUCK CLASSES KILLED IN THE KRUGER NATIONAL PARK (after Pienaar, 1969a)

Class	Lion	Leopard	Cheetah	Wild Dog
adult	113	2	0	4
non-adult	20	18	16	2

The waterbuck's commonest defence is simply to run or to hide in bush or long grass but there have been several witnesses to them taking refuge in water, particularly from wild dogs. One report described wild dogs killing a male while a cow and calf immersed themselves in water so that only the nostrils were on the surface.



Occasionally males fight back and a single hyaena pursuing a waterbuck has been seen to be put to flight. In Uganda, a large wounded bull killed eight dogs and a man before it was itself killed by a hunting party (U.G.R., 1952).

Like elands, subadult groups may rest together in a star formation. Although waterbuck have been recorded contracting anthrax, foot and mouth disease and rinderpest, it is rare for these diseases to play a major role in controlling numbers and they seem to be partially immune to the latter. Spinage (1969c) recorded 2,033 ticks on one adult male but this is not difficult to imagine for those who have suffered the ravages of pepper ticks.

Waterbuck breed throughout the year on the equator and the males regularly inspect females and make frequent clumsy attempt to copulate. Unreceptive females react by moving away, nodding the head with biting movements, which is also seen in juveniles and appears to be an appeasing gesture or greeting. The female's urine is frequently sampled by the male, which curls the lip in an exaggerated *flehmen* grimace (see drawing) as the urine runs over the nose and lips. If the female is in oestrus, the male rubs his chin on her rump and flank, investigates the inguinal area and strikes

out with the foreleg. Herbert (1972) noticed males wetting their chest and belly with urine while courting. In this connexion it is interesting that the related *Kobus megaceros* also urinates forward in the mating ceremony: "the male lowers his head as if he were going to dig the ground with his horns and he urinates in a jet between his front legs into the extended hairs at his throat and cheeks. With his beard dripping he walks over to the female and rubs his urine on her forehead and croup." (Walther in Grzimek, 1972). Perhaps undirected mounting by waterbuck males serves as a clumsy method of scent marking. It is interesting that both *K. megaceros* and *K. ellipsiprymnus* should resemble the red deer, *Cervus*, in having a thick neck ruff and that urine wetting of the ruff should first have been recorded in the red deer (Hediger, 1949). This habit may serve to deter other males from mating.

When the female is in oestrus she tends to hump her back and extend her tail to one side, and she shows considerable interest in the male, often sniffing into his groin and at the base of the horns, where Spinage has recorded the presence of a secretion that lubricates the horn. She may even attempt to mount the male when excited.

Males seek out females as soon as they have given birth and attach themselves until the *post partum* oestrus is over, and Spinage has been able to correlate this behaviour with an almost 100% reproductive rate.

The young are visited by the mother three or four times in 24 hours and suckling sessions last for about five minutes, during which time the mother induces the calf to defaecate by licking and presumably consumes its faeces.

"After each visit the dam abandons the calf as best she can, for although she may give it a signal when leading it, it will still follow her without a signal. Thus if it does not go to rest when the visit period is finished, the dam runs at speed through the bush and may shake it off this way, or she trots away when the calf's attention is diverted. The calf, finding itself alone, runs into the nearest thicket or long grass, where it remains until the next visit." (Spinage, 1969a)

In South Africa, Herbert (1972) described hidden calves emerging to follow a horseman. The mother's bleat is presumably not the only stimulus causing the calf to leave its shelter; also, regular visits may imply a time response, but such lack of discrimination is obviously dangerous and may encourage the observed high rate of calf mortality. Adamson (1972) saw a mother waterbuck defend her young against a cheetah by kicking.

Once the calf has joined the mother in a group it associates with other young and is rather playful. Verheyen (1955) described them provoking charging displays on the part of adult males. At this time the young often keep company with warthogs.

Weaning is completed at the age of six to eight months, at which time they begin to wander off. Growth is relatively slow and adult weights are not approached until the age of about three-and-a-half years.

**The Role of Visual Signals
and Face Patterns in
African Forest Monkeys
(Guenons) of the Genus
*Cercopithecus***

J. S. Kingdon

This paper explores the evolutionary origins of facial patterns in a single closely related genus of African monkeys. It sets out to identify the major factors that determine pattern formation and demonstrate the apparent role of facial signal patterns in the monkey's communication systems.

The mechanics of pattern elaboration are demonstrated through detailed examination of hair and skin pigmentation in closely related species. The effects of species-specific communication systems are sought in their distribution and evidence is presented for face patterns providing a mechanism that reinforces genetic isolation.

This paper has an entirely new and ecologically based approach to the problem of analysing optical communication and the evolution of signal devices in animals and more specifically in Old World simian primates. At a general level this paper is an essay exemplifying the role of patterns in animal communication and will be of interest to biologists, primatologists, naturalists and students of communication.

